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Thyasira dunbari n.sp. (Bivalvia: Thyasiridae) from the Canadian Arctic Archipelago

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LUBINSKY, I. 1976. *Thyasira dunbari* n.sp. (Bivalvia: Thyasiridae) from the Canadian arctic archipelago. J. Fish. Res. Board Can. 33: 1667–1670.

The shell morphology and area of distribution of *Thyasira dunbari* n.sp. is described and illustrated. This species differs from its northern relatives, especially *T. gouldi* Phil., by its high, bent forward shell, and thin, long edentulous hinge with massive callus. It occurs in the northernmost part of the Canadian archipelago and off East Greenland. It is a high arctic shallow-water species, which seems to be endemic in the Canadian–Greenlandic region.

LUBINSKY, I. 1976. *Thyasira dunbari* n.sp. (Bivalvia: Thyasiridae) from the Canadian arctic archipelago. J. Fish. Res. Board Can. 33: 1667–1670.

L'auteur décrit et figure la morphologie de la coquille et l'aire de distribution de *Thyasira dunbari* n.sp. Cette espèce diffère des espèces septentrionales apparentées, en particulier de *T. gouldi* Phil., par sa haute coquille recourbée vers l'avant et par sa charnière édentulée mince et longue avec callosité massive. Elle se rencontre dans la partie la plus septentrionale de l'Archipel canadien et au large du Groenland oriental. C'est une espèce d'eau peu profonde du Grand Nord qui semble endémique de la région canadienne–groenlandaise.

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A new *Thyasira* Dall, 1901 was present in the benthic material collected in the central Canadian arctic by Mr S. D. MacDonald of the National Museum of Canada, in 1951–54, and by the Arctic Biological Station, Fisheries and Marine Service, in 1962. This *Thyasira*, a species new to science, is described and illustrated below, and its distribution discussed.

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Thyasira dunbari n.sp.

Holotype — National Museum of Canada (NMC) 75803. Hole-in-Fog Bay, Isachsen, Ellef Ringnes Island, 78°47′N, 103°32′W. Depth 12.5 m, bottom mud. Collected by S. D. MacDonald, June 14, 1954.

Paratypes — NMC 75804. 15 specimens, data as for holotype.

Etymology — This species is named in honor

of Dr M. J. Dunbar, biologist, oceanographer, and explorer of the Canadian marine arctic.

Description — *Shell* — elongate, pyriform, high, asymmetrical in lateral view, expanded. Anterior part low arcuate; posterior high arcuate. Lunula and escutcheon well developed (Plate I, Fig. 1–6).

Size (mm) — *Holotype* — length (L) 6.2, height (H) 7.8, width (W) 4.8, H:L 0.77, W:L 1.25. *Paratypes* — L 6.2 (6.1–6.5), H 8.4 (7.8–8.6), W 4.8 (4.8–5.2), H:L 1.23 (1.16–1.29), W:L 0.75 (0.70–0.78). Two younger specimens, each 5 mm high, had H:L ratio 1.02 and 0.96, and W:L 0.61 and 0.64, respectively. Still younger specimens were not collected. However, check lines of growth on adults and measurements of the above two specimens, indicate that H:L of young is lower than for adults and they are more rounded and symmetrical (Plate I, Fig. 6).

Color — pale ochraceous buff, darker toward periphery of disc. Lines of arrested growth dark rust, distinct. Some specimens rust-colored, some dull salmon-pink.

Periostracum — rough, wrinkled, with irregular low folds at margin of disc.

Surface of shell — four shallow radial furrows, broadening toward periphery and ending in slight incurvations of disc margin. Largest furrow runs over middle of shell, ending in the posterior lower incurvation. Shallow furrow, usually marked by dark organic deposits, surrounds lunula. Two furrows on posterior part of shell, one of which surrounds escutcheon; second, slightly below, ends at the almost straight posterior margin.

Upper part of shell — extending from beaks to lower ends of lunula and escutcheon, is high, narrow and triangular, occupying almost half of shell height. Anterior and posterior margins of this part, formed by lunula and escutcheon, of equal length and meet at the beaks approximately at right angle (Plate I, Fig. 1, 2, 4).

Beaks — elevated, small, prosogyrate, tapering, slightly forward from middle of shell. Prodissoconch 160 μm. Lunula large, cordate, deeply set in, distinctly delimited; its bottom straight and flat (Plate I, Fig. 2, 3). Escutcheon curved, long, narrow, bottom flat, deeply sunken, delimited by a sharp crest (Plate I, Fig. 3, 6).

Hinge toothless, similar in both valves. Hinge plates thin and long. Anterior almost obsolete, posterior arcuate, narrow, of even width (Plate I, Fig. 5c). A strong spoon-shaped callus present at base of lunula (Plate I, Fig. 5a).

Lower part of shell — disc, extending down and forward in direction of higher increments; its posterior margin almost parallel to bottom of lunula.

Distribution — *Thyasira dunbari* occurs in the northwestern region of the Canadian archipelago, north from the M'Clure Strait–Lancaster Sound waterway (Fig. 7). This species was collected in fjords and bays at a depth of 10 to 70 m, on muddy bottoms, often close to the outwash fan of rivers.

Thyasira dunbari occurs also at the northern coasts of East Greenland (personal communication, W. K. Ockelmann, Helsingør Biological Station, Denmark).

It is a shallow-water species which seems to be endemic in the Canadian–Greenlandic high arctic region.

Discussion

Thyasira dunbari differs from other northern species of this genus by its extreme height, asymmetry, high hinge part, and its disc which is extended down and forward. It is larger than many other northern species of *Thyasira*, and darker colored.

To facilitate differentiation of *T. dunbari* from other northern *Thyasira* of similar size, a differential diagnosis between this species and *T. gouldi* Phil. is given below. The latter species, common in high latitudes, has been repeatedly discussed and illustrated and can therefore be reliably identified (Gould 1870; Ockelmann 1959, 1961; Sars 1878).

Differential diagnosis:

T. dunbari n.sp.	*T. gouldi* Phil.
Shell — high, pyriform, strongly asymmetric, transversally expanded. Anterior part low arcuate, its upper margin straight.	rounded, pyriform, slightly asymmetric. Anterior part high arcuate, upper margin slightly concave.
Size — height 7–9 mm, H:L 1.16–1.30, W:L 0.70–0.84.	height 4–7 mm, H:L about 1.0, W:L 0.50–0.70.

PLATE I. *Thyasira dunbari* n.sp. Holotype. Dimensions: L = 6.2; H = 7.8; W = 4.8 mm. FIG. 1. Side view, right valve; FIG. 2. Inside, left valve; FIG. 3. View from above. Paratypes: FIG. 4. Adult specimen, elongate. FIG. 5. Hinge: a, callus; b, ligament; c, posterior plate; d, posterior adductor. FIG. 6. Young specimen. Dimensions: L = 5.2; H = 5.3; W = 3.2 mm.

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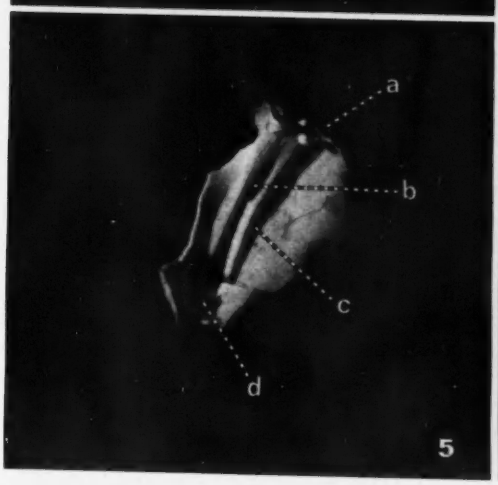
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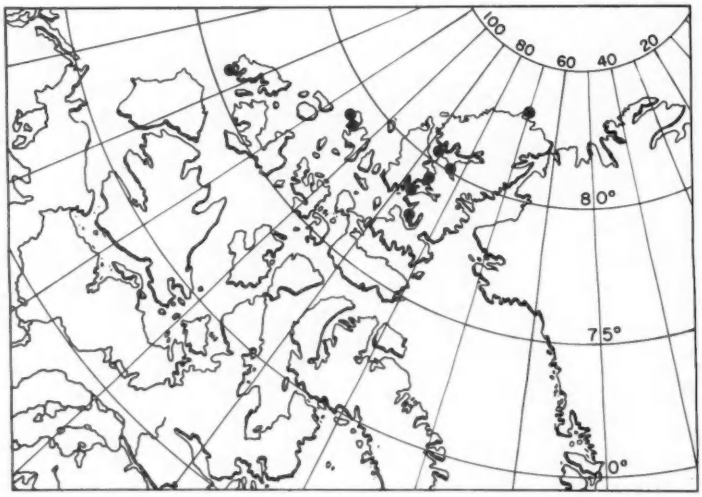

FIG. 7. Collecting sites of *Thyasira dunbari* n.sp. in the Canadian central arctic.

Surface — four shallow radial furrows, terminating in slight incurvations of margin.	two deep radial furrows on posterior part of shell, each terminating in deep incurvation of margin.
Disc — greatly extended down and forward.	rounded, slightly extended downward.
Upper part of shell — high, narrow and triangular, 30–50% total shell height. Its anterior and posterior margins (lunula and escutcheon) meet at right angle below beaks.	low and wide, 18–20% shell height. Its margins meet at an obtuse angle.
Lunula — large, cordate, well formed; bottom flat, straight.	not well formed and delimited; bottom uneven.
Escutcheon — long, narrow, sunken; bottom flat.	short, narrow; bottom usually protrudes slightly above surrounding ridge.
Prodissoconch — small, about 160 μm.	large, about 250 μm.
Hinge — edentulous, similar in both valves.	an irregular tooth vestige in right valve and a receptacle for it in left.
Posterior hinge plate — long, narrow, of even width.	short, winged.
Callus — strong, spoon-shaped.	a callous thickening of variable size and shape below beaks.

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I wish to thank Dr A. H. Clarke, National Museum of Canada, and Dr E. H. Grainger, Department of the Environment, Fisheries and Marine Service, Arctic Biological Station, for permission to use collections of their respective institutions; Mr W. Heck, photographer, Department of Zoology, University of Manitoba, for photographing the specimens. Special thanks are due to Dr W. K. Ockelmann, Biological Station, Helsingør, Denmark, for his interest in the present study.

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Toxicity of the Herbicides Dinoseb and Picloram to Cutthroat (*Salmo clarki*) and Lake Trout (*Salvelinus namaycush*)

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WOODWARD, D. F. 1976. Toxicity of the herbicides dinoseb and picloram to cutthroat (*Salmo clarki*) and lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33: 1671–1676.

In static tests of the toxicity of two herbicides, dinoseb (2,4-dinitro-6-sec-butylphenol) and picloram (4-amino-3,5,6-trichloropicolinic acid), to cutthroat (*Salmo clarki*) and lake trout (*Salvelinus namaycush*), the 96-h LC50s ranged from 32 to 1400 μg/liter for dinoseb and from 2050 to 8600 μg/liter for picloram. Decreasing pH from 8.5 to 6.5 increased the toxicity of dinoseb by a factor of 43 and decreased that of picloram by a factor of 0.5. Generally, toxicity increased with increasing water temperature. Sensitivity of both species of fish increased with water hardness in tests of dinoseb but was not affected by water hardness in tests of picloram. The toxicity of both chemicals was not changed by aging in water for up to 4 wk or by exposing the fish longer than 96 h. Rate of yolk sac absorption and growth of lake trout fry was reduced in flow-through tests at concentrations as low as 0.5 μg/liter dinoseb or 35 μg/liter picloram. Chronic toxicity of both compounds on early life stages of lake trout is more significant than might be anticipated on the basis of only acute tests with fingerlings.

WOODWARD, D. F. 1976. Toxicity of the herbicides dinoseb and picloram to cutthroat (*Salmo clarki*) and lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33: 1671–1676.

Lors d'essais statiques de toxicité de deux herbicides, dinoseb (2,4-dinitro-6-sec-butylphénol) et picloram (acide 4-amino-3,5,6,-trichloropicolinique), sur la truite fardée (*Salmo clarki*) et le touladi (*Salvelinus namaycush*), la CL50 après 96 h varie de 32 à 1 400 μg/litre pour le dinoseb et de 2 050 à 8 600 μg/litre pour le picloram. Un abaissement du pH de 8.5 à 6.6. augmente la toxicité du dinoseb par un facteur de 43 et diminue celle du picloram par un facteur de 0.5. En général, la toxicité augmente avec l'augmentation de la température de l'eau. La sensibilité des deux espèces de poisson augmente avec la dureté de l'eau dans les essais au dinoseb, mais n'est pas affectée par la dureté de l'eau dans les essais au picloram. La toxicité des deux produits chimiques n'est pas affectée par le vieillissement de l'eau jusqu'à 4 semaines ou par exposition des poissons pendant plus de 96 h. Le taux d'absorption du sac vitellin et la croissance d'alevins de touladi diminue dans des essais à flot continu à des concentrations aussi faibles que 0.5 μg/litre de dinoseb ou 35 μg/litre de picloram. La toxicité chronique des deux composés pour les premiers stades du cycle biologique du touladi est plus importante qu'on aurait pu le croire en se basant sur des essais aigus seulement avec des fingerlings.

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DINOSEB (2,4-dinitro-6-sec-butylphenol) is used in Wyoming to control ditch bank weeds and in Idaho to desiccate potato plants before potatoes are harvested (A. F. Gale personal communication). Picloram (4-amino-3,5,6-trichloropicolinic acid) is the main chemical control for two common and noxious weeds, Canada thistle and larkspur, in the intermountain area of the western United States (Alley et al. 1974). Use of dinoseb along ditch banks makes it a possible hazard to aquatic organisms. Picloram is poorly adsorbed and highly persistent in the soil; because it is mobile in soil water, it could contaminate ground or runoff water (National Academy of Sciences 1968). Investigation of the toxicity of these two chemicals to aquatic organisms in the intermountain west is not complete (Lipschuetz and Cooper 1961; Sanders 1969).

The present investigation was designed to assess the acute toxicity of dinoseb and picloram to cutthroat trout (*Salmo clarki*) and lake trout (*Salvelinus namaycush*) in waters differing in temperature, pH, and hardness and to determine chronic effects on survival, growth, and development.

Materials and Methods

FISH AND CHEMICALS

Cutthroat and lake trout were selected for this study because of their significance to sport fisheries

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in intermountain lakes and streams. Test fish were obtained from the Jackson (Wyoming) National Fish Hatchery and maintained according to the procedures reported by Brauhn and Schoettger (1975). Fish were held in 10 C spring water and acclimated to higher and lower test temperatures at the rate of 1 C/day. They were acclimated to waters for different pH, hardness, and alkalinity for 24 h. The weight of the fish ranged from 0.3 to 1.6 g in the acute mortality tests and from 0.9 to 6.3 g in the chronic mortality tests.

Technical grade dinoseb and picloram (active ingredient 95.8 and 90%, respectively) were obtained from Dow Chemical Company. All testing was conducted on the basis of active ingredient, and stock solutions were prepared in acetone within the 2 wk preceding treatment.

Acute Toxicity Tests

Acute toxicity tests were conducted under static conditions for 96 h according to procedures outlined by the Committee on Methods for Toxicity Tests with Aquatic Organisms (1975). Standard reconstituted soft water contained the following amounts of chemicals per liter of deionized water: 48 mg $NaHCO_3$, 30 mg $CaSO_4 \cdot 2H_2O$, 30 mg $MgSO_4$, and 2 mg KCl. Characteristics of standard reconstituted soft water were: pH, 7.0–7.4; hardness, 30–40 mg/liter (as $CaCO_3$); and alkalinity, 40–50 mg/liter (as $CaCO_3$). Water temperature was 10 C. Five fish were used per concentration, and toxicity was expressed as 96-h LC50s (concentration producing 50% mortality); 95% confidence intervals were obtained from regression analysis of mortalities and concentrations (Litchfield and Wilcoxon 1949).

The influence of temperature on acute toxicity was determined by testing fish in standard reconstituted water at 5, 10, and 15 C. Individual test containers were held in a water bath. Temperatures were maintained either with a cooling unit (5 and 10 C) or with a stock tank heater controlled by a thermoregulator (15 C).

The effects of pH on acute toxicity were measured at pH values of 6.5, 7.5, and 8.5, developed by adding the following reagent-grade buffer chemicals to 15 liters of standard reconstituted water: pH 6.5, 10 ml 1.0 N NaOH and 30 ml 1.0 M KH_2PO_4; pH 7.5, 19 ml 1.0 N NaOH and 20 ml 1.0 M KH_2PO_4; and pH 8.5, 12 ml 1.0 N NaOH and 40 ml 0.5 M H_3BO_3. The pH was checked and maintained daily throughout the 96-h tests.

The influence of water hardness on toxicity was determined in soft, hard, and very hard water. The method used to achieve these hardnesses was a slight modification of that recommended by the Committee on Methods for Toxicity Tests with Aquatic Organisms (1975). To maintain constant pH and alkalinity, I used 384 mg/liter, $NaHCO_3$ for all water hardness tests.

Effects of chemical aging on acute toxicity were determined in standard reconstituted water by the method of Marking and Dawson (1972). Separate solutions of dinoseb and picloram were allowed to age 4 wk before introduction of cutthroat trout. The 96-h LC50s of fresh solutions were compared with those of solutions aged for 4 wk.

Chronic Mortality Tests

Chronic toxicity of dinoseb and picloram was determined by using flow-through diluters (Mount and Brungs 1967), following the recommended procedure of APHA et al. (1971). The chemical metering device and calibration procedure were described by McAllister et al. (1972). Each species was exposed separately to 0, 30, 46, 86, 210, and 400 μg dinoseb/liter or 0, 380, 570, 1000 and 2400 μg picloram/liter. Thirty fish were exposed to each concentration of both chemicals. Fish were held and tested in 10 C spring water with pH of 7.4, total hardness of 162 mg/liter (as $CaCO_3$), and total alkalinity of 206 mg/liter (as $CaCO_3$). Exposure continued beyond 96 h until the mortality for 4 consecutive days was less than 5% of the fish remaining in each concentration. Toxicity was determined at 96 h and at termination of exposure.

Chronic Effects on Development and Growth

The procedures used to determine sublethal chronic effects were similar to those described for chronic mortality tests; however, the range of concentrations tested was lower and only lake trout were studied. Dinoseb concentrations were 0, 0.5, 1.6, 2.3, 4.9, and 10 μg/liter; and picloram concentrations were 0, 35, 75, 240, 500, and 1000 μg/liter. Twenty-five randomly selected eyed eggs were placed in each concentration of dinoseb 21 days before hatching, and in each concentration of picloram 10 days before hatching. Exposure continued through 60 days after hatching. Alevin survival, yolk absorption time, fry survival, and growth to age 60 days were determined. Yolk absorption time was the number of days (at 9.5 C) from median hatching date until the median date when yolk was totally absorbed; alevin survival was the percentage of alevins surviving yolk absorption; and fry survival was the percentage of fry surviving from yolk absorption to 60 days after hatching. Evaluation of growth was based on individual lengths and weights measured 60 days after the median hatching date.

The highest concentrations of dinoseb and picloram were analyzed by gas chromatography at 2, 4, and 6 wk. The calculated values for dinoseb were within the experimental variation of the analytical method, but the analyzed concentrations for picloram were low, due to loss by volatilization during sample storage (J. Johnson personal communication). Extraction and gas chromatographic determinations for dinoseb followed the procedures of Yip and Howard (1968). Analytical determinations for picloram were a modification of the procedure used by Bjerke et al. (1967).

I analyzed length and weight of fry at 60 days by analysis of variance and multiple means comparison

TABLE 1. Acute toxicity of dinoseb to cutthroat (*Salmo clarki*) and lake trout (*Salvelinus namaycush*) at different temperatures, pH's, and water hardnesses. (CI = confidence interval.)

Species	Temp (C)	pH	Water hardness	96-h LC50; 95% CI (μg/liter)	
			Temperature effects		
Cutthroat trout	5	7.2	soft	58	(48–70)
	10	7.2	soft	67	(56–81)
	15	7.2	soft	42	(32–54)
Lake trout	5	7.2	soft	135	(102–178)
	10	7.2	soft	44	(38–51)
	15	7.2	soft	36	(24–54)
			pH effects		
Cutthroat trout	10	6.5	soft	41	(34–49)
	10	7.5	soft	130	(89–189)
	10	8.5	soft	1,350	(1160–1580)
Lake trout	10	6.5	soft	32	(20–52)
	10	7.5	soft	77	(52–113)
	10	8.5	soft	1,400	(1170–1680)
			Water hardness effects		
Cutthroat trout	10	7.8	soft	550	(371–815)
	10	7.8	hard	340	(243–476)
	10	7.8	very hard	280	(207–317)
Lake trout	10	7.8	soft	280	(205–383)
	10	7.8	hard	140	(104–189)
	10	7.8	very hard	155	(107–224)

tests (least significant difference, LSD) to determine significant differences between treatments (Snedecor 1965).

Results and Discussion

ACUTE TOXICITY

The acute toxicity of dinoseb was affected most by changes in pH (Table 1). Decreasing pH from 8.5 to 6.5 increased toxicity of dinoseb to cutthroat trout and lake trout by factors of 33 and 43, respectively. Similar results were reported by Lipschuetz and Cooper (1961) for dinoseb and rainbow trout (*Salmo gairdneri*) in that decreasing pH from 8.0 to 6.9 increased toxicity by a factor of 5. Ionization of dinoseb, a weak acid (pKa = 4.4), at higher pH could decrease its ability to be transported across the gill and reduce toxicity (Maren et al. 1968). Also, under alkaline conditions, dinoseb may lose its phenolic characteristics and become less toxic (E. E. Kenaga personal communication). Further evaluation is needed to clearly define pH effects on dinoseb toxicity.

Toxicity of dinoseb to cutthroat and lake trout increased with increases in water temperature and hardness (Table 1). The influence of temperature and hardness on dinoseb toxicity was much less than that of pH, but was consistent for both species. Within the temperature, pH, and hardness ranges of cold-water habitats, combinations of low pH and high temperature and hardness would tend to maximize the sensitivity of these species to dinoseb.

Dinoseb is normally applied 3–4 times per summer when ditch bank weeds are a problem, and once immediately preceding the harvest of potatoes. Late-summer applications would correspond with periods of high water temperatures and low flow rates. Intermountain streams and lakes at the higher elevations generally have soft water, with a poor buffering capacity and low pH. Dinoseb would present the greatest hazard to cold-water fishes when applied in late summer to drainage or irrigation ditches above 6000 ft elevation. Increased hardness of irrigation water returning from potato fields would result in slight increases in dinoseb toxicity. Consequently other chemicals should be used in areas where the surface water pH is below 7.5.

Picloram, a derivative of picolinic acid, was also influenced by pH changes (Table 2). In contrast to dinoseb, picloram was more toxic in alkaline than in acidic water. Increasing pH from 6.5 to 8.5 increased the toxicity of picloram twofold to both species.

TABLE 2. Acute toxicity of picloram to cutthroat and lake trout at different temperatures, pH's, and water hardnesses. (CI = confidence interval.)

Species	Temp (C)	pH	Water hardness	96-h LC50; 95% CI (μg/liter)	
			Temperature effects		
Cutthroat trout	5	7.2	soft	6500	(5550–7610)
	10	7.2	soft	5000	(4360–5730)
	15	7.2	soft	4100	(3380–4970)
Lake trout	5	7.2	soft	3600	(2980–4350)
	10	7.2	soft	4250	(4000–4510)
	15	7.2	soft	2350	(1660–3340)
			pH effects		
Cutthroat trout	10	6.5	soft	8600	(7600–9730)
	10	7.5	soft	4700	(3940–5600)
	10	8.5	soft	4150	(3380–5100)
Lake trout	10	6.5	soft	4950	(4180–5870)
	10	7.5	soft	2700	(1820–4000)
	10	8.5	soft	2050	(1550–2710)
			Water hardness effects		
Cutthroat trout	10	7.8	soft	3700	(2890–4740)
	10	7.8	hard	3450	(2970–4000)
	10	7.8	very hard	3450	(2970–4000)
Lake trout	10	7.8	soft	2150	(1570–2940)
	10	7.8	hard	1550	(1180–2030)
	10	7.8	very hard	2100	(1550–2840)

The toxicity of picloram increased with increasing temperature but was not influenced by water hardness (Table 2). Combinations of high temperature and high pH would be expected to cause maximum toxicity to cutthroat and lake trout. However, the greatest hazard from picloram results from its persistence and mobility in soil water. Evans and Duseja (1973) reported that adsorption of picloram to soil is decreased by the low organic content characteristic of intermountain soil. They found that high pH increases picloram mobility in soil water, a factor that also increases toxicity to fishes. For protection of the cold-water fishery, picloram should not be applied on stream and lake slopes, flat marshy areas, or areas with high water tables.

Although biological inactivation and chemical decay cause detoxification of many chemicals in water (Marking and Dawson 1972), the toxicity of dinoseb and picloram to cutthroat trout remained unchanged after 4 wk of aging. Aging dinoseb for 0 and 4 wk resulted in 96-h LC50s of 71 and 87 μg/liter, respectively. Similar testing with picloram resulted in 96-h LC50s of 5800 and 5900 μg/liter, respectively. The stability of these herbicides in water suggests the use of picloram in areas of extensive leaching, or use of dinoseb along irrigation ditches, could contaminate aquatic habitats for many weeks after application.

CHRONIC MORTALITY TESTS

The toxicity of some compounds may be cumulative over periods of chronic exposure. Sprague (1969) and Eaton (1970) emphasized the importance of maintaining experimental exposures long enough to adequately define the lethal threshold concentration. The persistence of dinoseb and picloram increases the possibility of continuous aquatic habitat contamination. However, exposure of cutthroat and lake trout to dinoseb and picloram for 8–12 days did not cause cumulative mortality (Table 3). Increased exposure time resulted in only slight decreases in LC50s, and the LC50 for picloram and cutthroat trout did not decrease after 96 h. Chronic dinoseb and picloram exposure is not cumulative in terms of its direct lethal effects and will not result in increased cutthroat and lake trout mortality over that expected from short term exposures.

CHRONIC EFFECTS ON DEVELOPMENT AND GROWTH

Survival of lake trout fry in water containing 10 μg/liter dinoseb was 22% (Table 4). At

TABLE 3. Chronic mortality in cutthroat and lake trout exposed to dinoseb or picloram. (CI = confidence interval.)

Compound and species	Exposure time (*days*)	LC50 and 95% CI			
		96-h (*μg/liter*)		Terminal day (*μg/liter*)	
Dinoseb					
Cutthroat trout	10	152	(131–176)	125	(104–150)
Lake trout	10	79	(67–93)	65	(57–75)
Picloram					
Cutthroat trout	8	1475	(1240–1760)	1475	(1240–1760)
Lake trout	12	1850	(1630–2100)	1300	(1040–1630)

TABLE 4. Chronic effects of dinoseb on growth and development of lake trout.

Concn of dinoseb (*μg/liter*)	Yolk absorption[a] (*days*)	Alevin survival (%)	Fry survival (%)	Fry, 60-days posthatching		
				Survival (%)	Wt (*mg*)	Length (*mm*)
0	31	96	100	86	378	33
0.5	38	96	78	75	247[b]	30[b]
1.6	37	76	100	76	241[b]	30[b]
2.3	39	87	90	78	244[b]	30[b]
4.9	40	88	95	83	208[b]	28[b]
10.0	40	24	100	22	152[b]	25[b]

[a]Calculated from median hatch date to median yolk absorption date at 9.5 C.
[b]Significantly different from control group ($LSD_{0.05}$).

TABLE 5. Chronic effects of picloram on growth and development of lake trout.

Concn of picloram (*μg/liter*)	Yolk absorption[a] (*days*)	Alevin survival (%)	Fry survival (%)	Fry, 60-days posthatching		
				Survival (%)	Wt (*mg*)	Length (*mm*)
0	34	100	100	100	373	33
35	39	75	72	52	233[b]	28[b]
75	38	63	100	58	154[b]	26[b]
240	38	29	67	17	117[b]	23[b]
500	—	0	0	0	—	—
1000	—	0	0	0	—	—

[a]Calculated from median hatch date to median yolk absorption date at 9.5 C.
[b]Significantly different from control group ($LSD_{0.05}$).

dinoseb concentrations of 4.9 μg/liter or less, the survival of fry was similar to that of controls, but yolk absorption time was increased by 6–9 days; growth of fry was significantly ($P < 0.05$) lower than that of control fish, at all dinoseb concentrations. Although the concentration not affecting lake trout fry survival was between 4.9 and 10 μg/liter, dinoseb appears to affect growth of the fry at concentrations below 0.5 μg/liter. The lowest picloram concentration, 35 μg/liter, reduced fry survival and significantly inhibited growth ($P < 0.05$, Table 5). Most mortalities occurred during yolk absorption which was 4–5 days longer in picloram-treated fry. The no-effect concentration of picloram for lake trout is apparently below 35 μg/liter.

Other investigators (Mount and Stephan 1967, 1969; McKim and Benoit 1971, 1974) used a maximum acceptable toxic concentration (MATC) to assist in predicting "safe" concentrations of chemicals in aquatic ecosystems. These authors defined the MATC as the highest continuous exposure concentration that does not affect survival, reproduction, or growth. When the MATC

is divided by the 96-h LC50 for that species under similar test conditions, the resulting factor provides a base useful in extrapolating estimates of the MATC from 96-h LC50s for related species, or for other test conditions. These authors calculated the MATC's for malathion, copper, and the butoxyethanol ester of 2,4-D to be 0.02–0.22 of the 96-h LC50s for brook trout (*Salvelinus fontinalis*) and fathead minnows (*Pimephales promelas*). Mount and Stephan (1969) and McKim and Benoit (1971) showed that fry from exposed parents were no more susceptible to the chemicals than fry from unexposed parents.

I was unable to determine an exact no-effect concentration of dinoseb and picloram because growth was affected at the lowest levels tested. Therefore, the MATC's for these two compounds are below 0.5 for dinoseb and 35 μg/liter for picloram. The 96-h LC50s for dinoseb and picloram in water similar to that used in the chronic studies (Tables 1 and 2) were 77 and 2700 μg/liter, respectively. Dividing the approximate MATC by the appropriate LC50 value gives a factor of about 0.01, or less, for both chemicals. The National Academy of Science Committee on Water Quality Criteria (1973) was unable to recommend maximum water concentrations for dinoseb and picloram because too few data were available. The approximate factor estimated on the basis of the present study is sufficient, however, to arouse concern for chronic effects of dinoseb and picloram on salmonids. It should be better defined, however, by testing lower concentrations and other species, and according to simulated use patterns.

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Marine Mortality of Puget Sound Coho Salmon (*Oncorhynchus kisutch*)[1]

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MATHEWS, S. B., AND R. BUCKLEY. 1976. Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 1677–1684.

A model for natural mortality over the 18 mo of marine life of Puget Sound coho salmon (*Oncorhynchus kisutch*) is proposed, wherein the natural mortality rate M continuously decreases with increasing weight. Weight closely follows an increasing exponential function of marine age. The model is extended to account for ocean troll and sport fishing mortality and applied to data from marking studies of Puget Sound coho. The survival curve for marine life with only natural mortality declines rapidly for early ocean life and is quite flat over the ages fished. Recent high survival rates for hatchery coho released at a larger than normal size could be partially explained by this mortality model, although additional marking experiments are needed to separate the effects upon survival of size at release and time of release. The model applied to hatchery release-size strategy indicates that 70 g/fish might be optimal.

MATHEWS, S. B., AND R. BUCKLEY. 1976. Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 1677–1684.

Nous proposons un modèle pour la mortalité naturelle, sur une période de 18 mois de vie en mer, du saumon coho (*Oncorhynchus kisutch*) du Puget Sound, dans lequel le taux de mortalité naturelle M diminue continuellement avec l'augmentation de poids. Le poids suit de près une fonction exponentielle croissante de l'âge en mer. Nous élargissons le modèle pour expliquer la mortalité due à la pêche à la traîne et à la pêche sportive dans l'océan. Nous l'appliquons enfin à des données de marquage de saumons coho du Puget Sound. La courbe de survie pour la vie en mer, avec seulement la mortalité naturelle, baisse très rapidement au début de la vie océanique pour ensuite se stabiliser aux âges où les poissons sont pêchés. Ce modèle de mortalité peut expliquer partiellement les taux récents de haute survie pour des saumons coho d'élevage mis en liberté à une taille plus grande que la taille normale. Il faudra cependant des marquages supplémentaires pour isoler les effets sur la survie de la taille au moment de la mise en liberté et du temps de mise en liberté. Si l'on se base sur le modèle pour déterminer la taille à laquelle les poissons de pisciculture devraient être relâchés, on croit que 70 g serait la taille optimale.

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THIS paper presents a model of ocean mortality for coho salmon, *Oncorhynchus kisutch*, that assumes a rate of natural mortality inversely proportional to the individual weight of the fish. Recent survival data for marked Puget Sound hatchery coho are considered within the framework of the model.

The Fisheries

Ocean troll and sport fisheries catch Puget Sound coho during their last 4 mo in coastal waters from near the mouth of the Columbia River to the northern end of Vancouver Island. A few coho (<10%) normally remain in Puget Sound throughout their marine life, contributing to the sport fishery during the last 4–12 mo, depending on the minimum size limit which has varied over the years (Buckley 1969). Net fisheries in the Strait of Juan de Fuca and Puget Sound harvest the spawning migration during the last few weeks of marine life.

Marine Growth

Coho smolts are normally released from Puget Sound hatcheries in mid-April and average about 23 g (20 fish/pound). Their marine growth can be traced from several sources (Table 1). Seventy-two percent of the freshwater recoveries of yearling coho tagged in Saanich Inlet (British

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TABLE 1. Estimates of average lengths and weights of Puget Sound coho salmon (*Oncorhynchus kisutch*) at sea.

Approx. date	Location	Fork length (*cm*)	Wt g	Wt lb	Source
Apr. 15	Puget Sound hatchery release points	—	23	.05	Senn (1970a, b); Senn and Satterthwaite (1971)
Sept. 1	Saanich Inlet, B.C.	26	246	.55[a]	Heizer and Argue (1972)
Dec. 15	Saanich Inlet, B.C.	32	540	1.19[a]	Heizer and Argue (1972)
Feb. 1	Saanich Inlet, B.C.	34	681	1.50[a]	Heizer and Argue (1972)
June 15	Cape Flattery	54[a]	1905	4.20	Wash. Dep. Fish. troll catch statistics
Oct. 15	Puget Sound estuaries	68[a]	3823	8.20	Wash. Dep. Fish. Indian catch statistics

[a]Length–weight conversion data for sport- and troll-caught coho were used to convert Saanich Inlet average lengths to average weights, and to convert troll and Indian catch average weights to average lengths.

Columbia) during September, December, and February in 1970 and 1971 were recovered in Puget Sound streams, including hatcheries (Heizer and Argue 1972). Thus the mean lengths of the coho at time of capture in Saanich Inlet provide estimates of the size of Puget Sound coho after 4.5, 8, and 9.5 mo at sea. About 45% of Cape Flattery troll-caught coho are from Puget Sound, and this troll area has the greatest proportion of Puget Sound coho (Senn 1970a, b; Senn and Satterthwaite 1971). Average (1963–72) round weight per troll-caught fish[2] from catches on June 15 (opening date of the coho season) was used as an estimate of the size of Puget Sound coho after 14 mo at sea. The adult weight of Puget Sound coho was estimated from the 1963–72 average round weight of fish caught by Indian drag seines, traps, and set nets in estuaries of eight major Puget Sound rivers. These catches peak in mid-October, 18 mo after release of hatchery smolts.

A least squares regression of ln W (weight in grams) against t (time in months) gave the following relationship (Fig. 1):

$$W(t) = 44.6\ e^{.265t} \qquad (1)$$

The 95% confidence limits for the intercept, 21.2–92.9, included the release weight 23 g. An advantage of this relationship is its simplicity in later analysis.

[2]Washington State Department of Fisheries' bound statistical catch summaries from landing tickets, available in Olympia, Washington.

Mortality Model

We assumed that the instantaneous rate of natural mortality at sea is inversely related to individual weight and thus decreases with marine life exponentially, i.e.:

$$M(t) = c/ae^{gt} = ke^{-gt} \qquad (2)$$

Our reasoning for such a model is the assumption that marine natural mortality is mainly from predation; the larger a fish, the fewer the predators capable of eating it and the faster it is able to swim to avoid capture. Unfortunately intuition must substitute for hard facts on these points.

Ignoring at first the removal of 2-yr-old mature males after 6 mo, a cohort released April 15 would decline according to:

$$\frac{dN}{dt} = -M(t) \cdot N(t)$$

Substituting from (2) for $M(t)$ and solving with initial conditions that $N = N_o$ when $t = o$,

$$N(t) = N_0 \exp\left[\frac{k}{g}(e^{-gt} - 1)\right] \qquad (3)$$

Of the two parameters in this relationship, g is the exponent in the weight at age function and k can be estimated if total catch and escapement

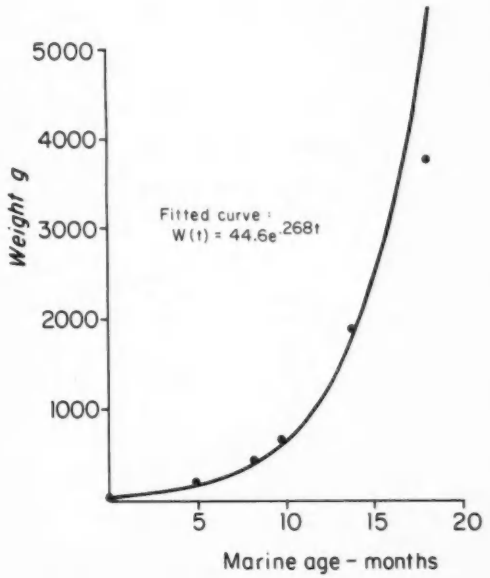

FIG. 1. Marine growth of Puget Sound coho salmon (*Oncorhynchus kisutch*).

data for a marked lot are available:

Let C = troll and sport catch in the 4 mo preceding maturity (June 15–October 15);

F = instantaneous mortality rate per month due to ocean troll and sport fishing over the last 4 mo;

S = number of mature 3-yr-old survivors following the ocean fisheries (net catch plus spawning escapement).

Thus, with ocean troll and sport fishing in the last 4 mo,

$$\frac{dN}{dt} = -[F(t) + M(t)]\cdot N(t) \qquad (4)$$

where:

$$F(t) = 0 \text{ if } t \leqslant 14$$

$$F(t) = F \text{ if } 14 \leqslant t \leqslant 18$$

The solution to (4) again with $N = N_o$ when $t = o$ is,

$$N(t) = N_0 \exp\left[\frac{k}{g}(e^{-gt} - 1)\right] \text{ for } t \leqslant 14,$$

and

$$N(t) = N_0 \exp\left[\frac{k}{g}(e^{-gt} - 1) - F(t - 14)\right] \text{ for } 14 \leqslant t \leqslant 18.$$

Since

$$C = \int_{14}^{18} F\cdot N(t)\cdot dt$$

then

$$C = FN_0 e^{-(k/g)} \int_{14}^{18} e^{(k/g)e^{-gt} - F(t-14)} dt \qquad (5)$$

and

$$S \cong N(18) = N_0 \exp\left[\frac{k}{g}(e^{-18g} - 1) - 4F\right] \qquad (6)$$

Equations (5) and (6) are a pair of equations in two unknowns, k and F, that can be solved simultaneously by trial and error. A FORTRAN computer program using a numerical integration subroutine was written for this.

The model can be extended to account for the exodus of 2-yr-old mature males, which are so small a fraction of the total Puget Sound population that they can, practically speaking, be ignored. The extension is presented, however, for completeness.

Assuming that those members of an initial cohort destined to mature as 2-yr-olds grow and survive at the same rates as the remaining fish (actually there is evidence that they grow somewhat faster: R. Hager, Washington Department of Fisheries, personal communication), then if J is the return of 2-yr-old males after 6 mo, the initial cohort N_o is made up of two segments:

$$N_o = N_o' + J/\exp\left[\frac{k}{g}(e^{-6g} - 1)\right]$$

The first term, N_o', represents the 3-yr returning segment and the second term represents the 2-yr segment.

Equations (5) and (6) then become:

$$C = F\left\{N_o - J/\exp\left[\frac{k}{g}(e^{-6g} - 1)\right]\right\} e^{-(k/g)} \times \int_{14}^{18} e^{(k/g)e^{-gt} - F(t-14)} dt \qquad (7)$$

$$S = \left\{N_o - J/\exp\left[\frac{k}{g}(e^{-6g} - 1)\right]\right\} \times \exp\left[\frac{k}{g}(e^{-gt} - 1) - 4F\right] \qquad (8)$$

Slight modification of the previously mentioned computer program gave approximate solutions for k and F.

Application of the Model

Three brood years of coho (1964, 1965, and 1966) from Puget Sound hatcheries were marked (ventral fin-maxillary bone). Mark sampling in

TABLE 2. Results of fin-marking and fishery sampling for 3 brood yr of coho from Skykomish River, Issaquah Creek, Green River, Puyallup River, and Minter Creek hatcheries (from Senn 1970a, b; Senn and Satterthwaite 1971).

	1964	1965	1966
No. marked and unmarked coho released[a]	4,319,525	4,094,732	4,443,166
Mark	LVRM	RVLM	LVRM
Avg size at release	20.2 g	24.2 g	25.6 g
Estimated no. marked and unmarked coho caught in last year of life[b]			
British Columbia troll	39,448	178,794	94,505
Washington troll	26,600	17,622	28,354
Oregon troll	1,354	1,006	503
California troll	0	90	52
British Columbia net	48,684	65,042	45,550
Washington net	40,519	53,832	48,801
Washington ocean sport	13,158	20,011	23,426
Washington Puget Sound sport	7,598	13,958	10,759
Washington river sport	2,824	2,836	1,006
Oregon sport	310	194	0
California sport	0	0	26
Spawning escapement of 3-yr-olds	42,294	96,684	109,973
Total catch plus escapement of 3-yr-olds	222,789	450,069	362,955
(Catch plus escapement/release no.) × 100	5.16%	10.99%	8.17%
Spawning escapement of 2-yr-olds	3,437	10,749	9,127

[a]About 10% of the hatchery-released coho were marked each year.
[b]It was assumed that marked coho survived at a level of 80% of unmarked fish. Consequently, contribution rates of marked fish were multiplied by 1.25 in estimating fishery recoveries of unmarked fish.

all major fisheries led to estimates of total fishery contribution (Senn 1970a, b; Senn and Satterthwaite 1971). Table 2 summarizes the results for coho that received a common mark each year at five central Puget Sound hatcheries.

Average values over the 3 brood yr were:

$$C = 158{,}257$$
$$S = 186{,}016$$
$$J = 7{,}771$$
$$N_u = 4{,}285{,}805.$$

With $g = 0.268$, estimates of k and F were:

	k	F
from Equations (5) and (6):	0.682	0.153
from Equations (7) and (8):	0.679	0.153

Thus, the inclusion of the 2-yr maturing fish does not appreciably change the estimated survivorship function for 3-yr maturing fish (Fig. 2).

Survival of Delayed Release Coho

If mortality is size dependent, as assumed in this model, then hatchery fish released at a larger than normal size would be expected to survive at a substantially higher rate, other conditions remaining the same. For example, a cohort released at 3 times their normal size (68 g) on July 1 would have a relative abundance of about $1/N(2.5) = 0.290$ if there were negligible mortality occurring in the hatchery during the extra 2.5 mo. If the survivorship of a cohort of 23 g coho is 0.081 in terms of contribution to the fishery and escapement (Table 2), then the predicted survivorship of the delayed lot would be:

$$\frac{0.081}{0.290} = .279$$

Similarly a lot released on June 1 at twice the normal size should have a survivorship of:

$$\frac{0.081}{0.432} = .188$$

Two mark and recovery experiments support these predicted increases in survival, although neither was entirely satisfactory. Too little effort

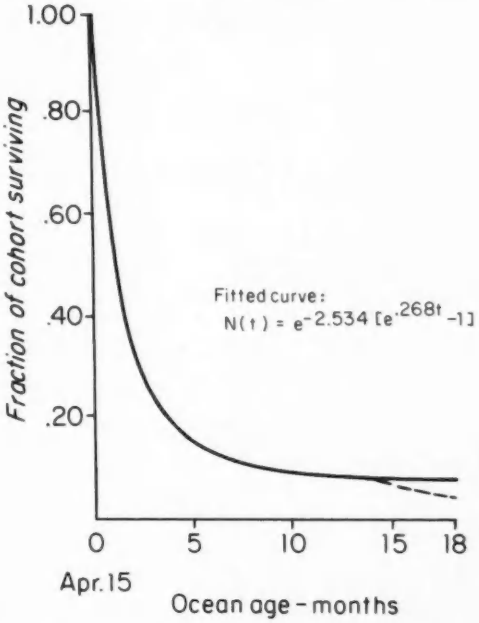

FIG. 2. Survivorship curve for Puget Sound hatchery coho salmon, assuming M inversely proportional to individual weight. (Dotted portion indicates the curve with ocean troll and sport fishery mortality imposed on natural mortality.)

was put into mark recovery, and the experimental design did not permit separation of the effects of time of release, size at release and distribution at sea. Both experiments were done at Minter Creek Hatchery, where the survival of coho was average for five Puget Sound hatcheries (Table 3). All fish were tagged with Bergman-Jefferts coded-wire tags (Bergman 1968).

1968 BROOD

Two groups of fish were released, a control group on April 1, 1970 (mean weight 21 g) and a delayed group on June 29 (mean weight 53 g) (Table 4). The Canadian coastal troll and net fisheries were not sampled. However, estimates were made of the fish taken in these fisheries as described in the footnotes to Table 4. The escapement was inadequately sampled so that the return estimates are probably low. Overall survival estimates were 2.3% for the normal release compared with 17% for the delayed release. These results are probably biased by inadequate sampling for marks. Survival of the delayed group, however, was clearly several times that of the control, as predicted by the model.

TABLE 3. Rates of return to five Puget Sound hatcheries, 1964–66 brood years. (Percentage return to hatchery rack as 3-yr-old adults.) (Senn 1970a, b and Senn and Satterthwaite 1971.)

	1964 brood	1965 brood	1966 brood
Green River	0.82%	4.52%	2.15%
Issaquah Creek	1.24%	1.61%	1.45%
Minter Creek	1.20%	1.24%	1.93%
Puyallup River	1.70%	2.92%	2.50%
Skykomish River	1.11%	1.19%	1.69%

1970 BROOD

Four groups of fish were released: a control on May 1 (25 g) and three delayed groups on June 1 (30 g), July 5 (45 g), and August 1 (50 g) (Table 5). Again the results are incomplete because the Canadian fisheries were not sampled. The results are further complicated because the proportion of recoveries in the Washington fisheries is strongly dependent on time of release. The later the release date, the greater the tendency to remain within Puget Sound and contribute to the sport fishery. How this affects the comparison of survival based upon total catch and escapement is uncertain. For comparison with the control, the average for the three delayed groups may be appropriate. The comparative figures were control, 7.88%, and delayed, 18.88%. The high survival of group 2, released 1 mo after the control, at only slightly larger size, indicates the probability that time of release as well as size influences survival. Obviously an experiment crossing time and size must be run to test the hypothesis adequately.

One application of this model is in selecting target release-size for Puget Sound hatcheries. Water flow is the major factor limiting the total weight of salmon that can be released from a hatchery. If several assumptions are met, the survivorship function can be used to relate the number of coho reaching ocean fishery recruitment age per kilogram released, to size at release. These assumptions are: 1) the weight of coho 23 g and larger that can be held per unit of water flow does not vary with average fish size; 2) coho will grow in a hatchery at the same exponential rate as at sea according to $W(t) = 23 \exp [0.268\ t]$; 3) there is negligible mortality of fish held in the hatchery from April 15 ($t = 0$) to time t of release, and thus the survival rate from release to recruitment is $N(14)/N(t)$. Accordingly, Table 6 indicates that a release size of about 70 g might be optimal. Final hatchery strategy would depend, of course, upon many

TABLE 4. Estimated survival and fishery contribution of 1968 brood control and delayed release groups of coho from Minter Creek Hatchery.

	Control	Delayed
No. tagged coho released	68,206	69,152
Date released	Apr. 1	June 29
Avg size at release	21 g	52 g
Estimated no. tagged coho caught in last year of life[a]		
British Columbia troll	(39)[b]	(1,247)[b]
Washington troll	14	445
British Columbia net	(504)[c]	(904)[c]
Washington net	657	2,145
Washington ocean sport	88	1,028
Washington Puget Sound sport	242	5,685
Spawning escapement of 3-yr-olds	39[d]	316[d]
(Catch plus escapement/release no.) × 100	2.3%	17.0%

[a]Actual mark recoveries were multiplied by 1.075, since Bergman (1968) found that wire-tagged coho returned at a rate 7% less than a tetracycline control lot.

[b]Based on the average 1964–66 brood ratio of Washington:Canadian troll contributions.

[c]Based upon the Washington net catch less Carr Inlet recoveries, adjusted by the ratio of Washington:Canadian net fishery recoveries of the 1964–66 broods. The Carr Inlet fishery is a special gillnet and purse seine fishery begun in 1971 near the mouth of Minter Creek to increase harvest of hatchery salmon.

[d]Known rack recoveries. An unknown number was allowed to pass upstream without sampling for tags.

TABLE 5. Survival and fishery contribution of 1970 brood control and delayed release groups of coho from Minter Creek Hatchery.

	1970 brood			
		Delayed		
	Control	Lot 2	Lot 3	Lot 4
No. tagged coho released	13,686	18,057	17,442	16,823
Date released	May 1	June 1	July 5	Aug. 1
Avg size at release	25 g	30 g	45 g	50 g
Estimated no. tagged coho caught in last year of life[a]				
British Columbia troll	(277)[b]	(1,279)[b]	(629)[b]	(280)[b]
Washington troll	99	455	225	100
British Columbia net	(226)[c]	(1,024)[c]	(356)[c]	(225)[c]
Washington net	369	1,309	575	534
Washington ocean sport	12	248	81	70
Washington Puget Sound sport	41	274	657	973
Spawning escapement of 3-yr-olds	52	224	200	240
(Catch plus escapement/release no.) × 100	7.9%	26.6%	15.6%	14.4%

[a]A mark effect factor of 1.075 was used in the estimates of catch and escapement.

[b]Based on the average 1964–66 brood ratio of Washington:Canadian troll contributions.

[c]Based upon the Washington net catch less Carr Inlet recoveries adjusted by the ratio of Washington:Canadian net fishery recoveries of the 1964–66 broods.

TABLE 6. Predicted relationship between size at release of Puget Sound coho and recruitment to ocean fisheries.

Size at release		Time t in months		Survival rate to recruitment	No. fish recruited/
g/fish	fish/1000 g	(April 15 = 0)	N(t)	N(14)/N(t)	1000 g released
23	43.48	0.00	1.000	.084	3.65
30	33.33	0.99	.554	.152	5.07
40	25.00	2.06	.340	.247	6.18
50	20.00	2.90	.254	.331	6.62
60	16.67	3.58	.209	.402	6.70
70	14.28	4.15	.168	.500	7.14
80	12.50	4.65	.165	.509	6.36
100	10.00	5.48	.142	.592	5.92
150	6.67	7.00	.117	.718	4.79
200	5.00	8.07	.106	.792	3.96
300	3.33	9.58	.096	.875	2.91
400	2.50	10.65	.092	.913	2.28

TABLE 7. Comparison of Puget Sound and Columbia River hatchery coho mortality models.[a]

	Columbia River	Puget Sound
% of cohort of smolts that survive first 6 mo at sea	9–10%	13%
% of those that survive for 6 mo and then return as jacks	3–4%	1%
% of those remaining in the ocean after 6 mo that survive to the time of recruitment to the ocean fisheries	55–65%	64%
% of initial cohort at sea after 12 mo	6%	9%
% of those that survive 12 mo at sea and are then caught by ocean fisheries	68–70%	42%
% of those alive at time of recruitment that survive the ocean fisheries	19%	52%
% of cohort remaining after ocean life	1%	4%

[a]Cohorts released similarly about April 15 at about 23 g/fish.

other operational considerations, such as costs, other species being raised jointly and relative values of fish in specific fisheries.

Discussion

The mortality model presented in this paper predicts mortality of resident Puget Sound coho of 11% as compared to 48% estimated from tagging (Mathews and Buckley 1974) for the period January 31–May 15. The tagging estimate was based on returns from relatively few tags, however, and thus the variance was high. Mathews and Buckley (1974) assumed no fishing loss from January to May because the coho were less than the minimum legal size limit for most of the period. Perhaps there was loss from hooking, unknown to Mathews and Buckley, which would bias this previous estimate of mortality upward. Buckley (1969) indicates that the "resident" segment of the Puget Sound population had been undergoing a rather serious decline compared to the ocean-going segment for the previous two decades and discussed several possible reasons. Thus, there may be more intensive mortality factors operating within the Sound than the ocean. At this stage, however, particularly because of the very high survival seen in delayed groups which apparently contributed highly to the resident populations, we would rate the previous estimate of natural mortality based on the two-stage tagging as probably too high.

Published estimates of ocean mortality, exclusive of coastal mortality for sockeye, pink, chum,

and chinook, are rather constant, varying from 20 to 28%/yr (Parker 1962; Fredin 1965). Our model predicts a mortality rate of 39% during the last 12 mo of sea life for Puget Sound coho. For pink salmon, Parker (1968) published a coastal mortality rate of 2–4%/day for about the first 40 days of sea life, followed by a rate of 0.4–0.8% for the remaining 410 days. For our coho model, applying a two-stage exponential decline to the survival fractions $N_{''} = 1.0$, $N(1.33) = 0.467$ and $N(18) = 0.081$, average daily losses would amount to 2%/day for the first 40 days and 0.3%/day for the remaining 507 days.

Lander and Henry (1974) presented a model for mortality of 1965 and 1966 brood Columbia River hatchery coho that assumed a high constant rate of mortality for the first 6 mo and a lesser, constant rate for the last 12 mo. Their model and ours give quite similar estimates of natural mortality, considering the different analytical approaches (Table 7). Our model predicts a lower mortality for the first 6 mo. Puget Sound has a lower proportion of jacks and a lower ocean exploitation rate, both of which yield a contribution to a greater predicted 3-yr-old return. The Columbia River data were based upon average figures for four groups marked according to the location of the hatchery. Averaged, the survival was less than for the Puget Sound fish. The largest group of Columbia River fish from the middle river hatcheries survived at a rate comparable to the Puget Sound fish, but with a substantially higher ocean catch to adult return ratio.

Acknowledgments

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Acute and Chronic Toxicity of Copper to Four Species of *Daphnia*

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WINNER, R. W., AND M. P. FARRELL. 1976. Acute and chronic toxicity of copper to four species of *Daphnia*. J. Fish. Res. Board Can. 33: 1685–1691.

The sensitivity of *Daphnia magna*, *D. pulex*, *D. parvula*, and *D. ambigua* to acute and chronic copper stresses was evaluated under laboratory conditions. Using 72-h LC50 values as the index, the two larger species were significantly less sensitive to an acute copper stress than were the two smaller species. All four species exhibited reductions in survival at Cu concentrations >40 μg/liter. *Daphnia magna* exhibited a decrease in the instantaneous rate of population growth (r) at Cu concentrations >60 μg/liter; r decreased in the other three species at concentrations >40 μg/liter. *Daphnia ambigua* produced significantly smaller broods at Cu concentrations >40 μg/liter, whereas mean bood sizes did not decrease in *D. pulex* and *D. parvula* until the Cu concentration exceeded 60 μg/liter. *Daphnia magna* did not exhibit any reduction in mean brood size related to copper concentration; reproduction in this latter species was inhibited only as a consequence of females dying before they reached reproductive maturity at concentrations >80 μg/liter. Application factors, based on the highest concentration that did not reduce survival and 72-h LC50 values, ranged from 0.47 to 0.59 and were not significantly different for the four species. We concluded that the four species do not differ in their susceptibility to a chronic copper stress.

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Les auteurs ont évalué la sensibilité de *Daphnia magna*, *D. pulex*, *D. parvula* et *D. ambigua* à des stress aigus et chroniques causés par le cuivre dans des conditions de laboratoire. Les valeurs de CL_{50} après 72 h servant d'indice, les deux plus grandes espèces sont nettement moins sensibles à un stress aigu causé par le cuivre que ne le sont les deux plus petites espèces. Les quatre espèces ont toutes une survie moindre à des concentrations de Cu > 40 μg/litre. *Daphnia magna* montre une diminution du taux instantané de croissance de population (r) à des concentrations de Cu > 60 μg/litre; r diminue chez les trois autres espèces à des concentrations > 40 μg/litre. *Daphnia ambigua* produit des portées significativement plus petites à des concentrations de Cu > 40 μg/litre, alors que la grosseur moyenne des portées ne diminue pas chez *D. pulex* et *D. parvula* tant que la concentration de Cu ne dépasse pas 60 μg/litre. *Daphnia magna* n'accuse pas de diminution de grandeur moyenne de la portée en relation avec la concentration a'aigu; chez cette dernière espèce, la reproduction est inhibée seulement comme conséquence des mortalités des femelles avant qu'elles n'atteignent la maturité sexuelle à des concentrations > 80 μg/litre. Les facteurs d'application, basés sur la plus haute concentration qui ne diminue pas la survie et sur les valeurs de CL_{50} après 72 h, s'étalent de 0.47 à 0.59 et ne diffèrent pas de façon significative pour les quatre espèces. Nous concluons que les quatre espèces ne diffèrent pas dans leur susceptibilité à un stress chronique causé par le cuivre.

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VIRTUALLY all of the toxicological work on planktonic invertebrates has dealt with a single species, *Daphnia magna* (Kemp et al. 1971). *Daphnia magna* has a limited geographical range and even within this range it is confined to small bodies of water (Brooks 1957). Since *D. magna* is not a frequent component of zooplankton communities, continued use of this species in research designed to formulate water-quality standards can be justified only if it can be demonstrated that *D. magna* has a sensitivity comparable to that of more widespread, important members of zooplankton communities. One of the objectives of this study was to compare the sensitivity to copper of *D. magna* with that of three more widespread species: *D. pulex*, *D. parvula*, and *D. ambigua*.

The ability to predict safe concentrations for chemicals is complicated by the necessity to take into account the sensitivity of a species throughout several generations. This idea is continuously compromised because of the immediate need for setting water-quality standards and the difficulty

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in maintaining many species under laboratory conditions. It has been suggested that the ratio between chronic and acute toxicity of a toxicant (the application factor of Mount 1968; and Mount and Stephan 1969) is relatively constant for closely related species. If this concept were proven valid, the factor could be used to extrapolate from the acute response of one species to the chronic response of another. Although there are some published data on application factors in fish, there are no such data available for daphnids. Therefore, a second objective of the present study was to evaluate the application-factor concept as it applies to daphnids.

Materials and Methods

All bioassays, both acute and chronic, were initiated with newborn daphnids (12 ± 12 h old). Animals were maintained in local pond water (total alkalinity 100–119 mg/liter; total hardness 130–160 mg/liter as $CaCO_3$). Dissolved O_2 concentrations varied between 8.7 and 11.4 mg/liter (95–125% saturated) and pH varied between 8.2 and 9.5 during the course of the experiments. All animals were maintained in environmental chambers at 20 ± 1 C on a 15-h photoperiod at approximately 32.29×10^2 lx of illumination. All stock and experimental animals were fed a diet of vitamin-enriched algae (*Chlamydomonas reinhardii*). Algae were cultured in Bold's basal medium (Nichols and Bold 1965) with vitamins added at the concentrations suggested by Murphy (1970). Algae were concentrated by centrifuging through a nonmetallic, continuous-flow centrifuge. This concentrate was adjusted in volume such that it had an absorbance of 1.5 at a wavelength of 665 nm. Copper was added to the algae cultures as $CuSO_4 \cdot 5H_2O$. A fresh stock solution of 100 mg Cu/liter was made up in double, glass-distilled water, on each day of use. Copper content of the distilled water, as determined by atomic-absorption spectroscopy, using an APDC-MIBK extraction method (Analytical Quality Control Laboratories 1971), was less than 1.0 μg/liter. Test concentrations were prepared by diluting appropriate aliquots of the stock solution in pond water.

Each experiment was initiated with a cohort of 10 newborn animals each in copper concentrations of 0, 20, 40, 60, 80, 100, 120, and 140 μg/liter. Each animal was maintained individually in 40 ml of pond water in a glass beaker and was fed three drops of the algal concentrate daily; this averaged 0.34 mg, dry wt, or 0.31 mg, ash-free dry wt, of algae per animal per feeding. Animals were examined daily, and young were counted and discarded until all experimental animals were dead (i.e. exhibited no movement). Animals were transferred at 3-day intervals to clean beakers containing fresh pond water. Three experiments, started at different times, were run for *D. magna* and two experiments were carried out for each of the other three species. Statements in the text relative to statistical significance always refer to the 0.05 probability level or less.

Day 3 of each experiment provided data for calculating a 72-h LC50 value by probit potency analysis (Finney 1971). A 72-h LC50 was arbitrarily used because the animals were transferred to fresh medium at 72-h intervals. There is no reason to believe that use of the more conventional 96-h LC50 would alter conclusions as to relative sensitivity of the species. Inter- and intraspecific comparisons of LC50 values were made only when the respective dose–response curves were demonstrated to be parallel (Finney 1971).

Three indices were used to assess the impact of copper on the organisms: 1) survivorship curves, 2) number of young per brood, and 3) r, the instantaneous rate of population growth.

Differences in survivorship curves were analyzed by chi-square analyses (Mantel 1966) using a computer program developed by, and available from: Carl Hacker, Department of Public Health, University of Texas, Austin, Tex.

Mean brood sizes at different copper concentrations were compared by a randomized complete block design analysis of variance with mean separation accomplished by Duncan's new multiple range test (Duncan 1955). Cumulative mean brood sizes were compared throughout the life span of the cohorts by running such analyses consecutively, from the first brood, through each brood, until the last brood produced in the experiment had been incorporated into the analysis. In other words, the experiment "was stopped" after each brood had been produced to determine what difference, if any, existed in cumulative mean brood sizes at the different copper concentrations.

The combined impact of a stress on longevity and reproductive output can be evaluated by examining changes in r, the instantaneous rate of population growth. We have calculated r, for each cohort, in each experiment, by solving for r in the equation:

$$1 = \Sigma P_i \cdot m_i \cdot e^{-ri}$$

where: e is the base of the natural logarithm, r is the instantaneous rate of population growth, P_i is the proportion of female survivors of age i, m_i is the mean number of progeny per female of age i, and i is age in days. Significant differences were determined by randomized complete-block design analysis of variance with mean separation accomplished by Duncan's new multiple range test (Duncan 1955).

Results and Discussion

Acute Toxicity of Copper

Data from the three experiments with *D. magna* and the two experiments with *D. ambigua* were combined to give a single best-estimate of an LC50 value for each species, since all of the dose–response curves were parallel. In the case of *D. pulex* and *D. parvula*, dose–response curves within each of the two experiments were not parallel. One dose–response curve for each of these species was, however, parallel to the

TABLE 1. Acute toxicity (72-h LC50 in micrograms per liter) of copper to four species of *Daphnia*. LC50 values sharing an underline are not significantly different ($P \leq 0.05$) as determined by Duncan's new multiple range test (Duncan 1955).

D. magna	*D. pulex*	*D. parvula*	*D. ambigua*
86.5[a]	86.0	72.0	67.7[b]
	54.0[c]	57.0[c]	

[a]Calculated from the pooled data of three experiments.
[b]Calculated from the pooled data of two experiments.
[c]LC50 values from nonparallel, dose–response curves which were not used in the mean separation.

TABLE 2. Vital Statistics for three chronic copper toxicity tests with *D. magna*.

Cu concn (μg/*liter*)	$\bar{x}$ Longevity (*days*)			Total young per			$\bar{x}$ Brood size		
	Exp 1	Exp 2	Exp 3	Exp 1	Exp 2	Exp 3	Exp 1	Exp 2	Exp 3
0	79.1	93.2	108.5	2314	3223	3287	10.6	13.1	12.3
20	99.6	99.7	91.7	3180	3863	2850	12.5	14.6	12.9
40	94.2	82.7	106.1	3329	3394	3110	13.3	15.2	13.1
60	45.3	48.8	69.0	1689	2150	2328	13.7	16.5	13.2
80	11.0	22.2	20.6	464	364	696	10.8	14.0	14.2
100	7.5	2.7	3.0	0	26	14	—[a]	13.0	7.0
120	3.1	0.3	0.4	0	0	0	—[a]	—[a]	—[a]

[a]No reproduction occurred.

dose–response curves of *D. magna* and *D. pulex*. Potency analysis was used to compare the LC50 values from those dose-response curves that were parallel (Table 1). The LC50 values were not significantly different for the two largest species (*D. magna* and *D. pulex*) nor for the two smallest species (*D. parvula* and *D. ambigua*). The two largest species were, however, significantly less sensitive to an acute copper stress than were the two smallest species (Table 1).

EFFECT OF CHRONIC COPPER EXPOSURES ON SURVIVORSHIP

The results of chi-square analyses of survivorship curves for the four species are encouragingly consistent. Survivorship curves at 20 and 40 μg/liter were never significantly different from those of control animals. With one exception, all survivorship curves at concentrations of 60 μg/liter or above were significantly different from that of control animals. The one exception was the second chronic test with *D. ambigua* where survivorship differed from that of control animals only at 80 and 100 μg/liter. The longevity of all animals, including the controls, was considerably reduced in experiment 2 with *D. ambigua*. This disparity between experiments did not occur with the other three species.

The reproducibility of life-history statistics is especially evident in the three chronic toxicity experiments with *D. magna* (Table 2). The first chronic test was in January 1974, the second in June 1974, and the third in January 1975. This reproducibility implies a rather uniform gene pool in the experimental animals (relative to copper sensitivity) and good reproducibility in the test system. If most of the variability is in individual-animal response, rather than in test conditions, a better impression of population response is achieved by combining the survivorship curves from the separate experiments for each species. This is done for each of the four species in Fig. 1. In these curves the more rapid die-off of all species in the 60 μg/liter copper solution indicates a significant increase in toxicity between 40 and 60 μg/liter. If current theory is correct (Stiff 1971; Pagenkopf et al. 1974), there must have been a saturation of the complexing capacity of the pond water within this range and a significant increase in the concentration of cupric ions.

These experiments show that the impact of a chronic copper stress on survival is not significantly different for these four species of *Daphnia*. If, however, the chronic experiments had been terminated at the end of 3 wk, as done by Biesinger and Christensen (1972), *D. magna* would have appeared to be less sensitive since

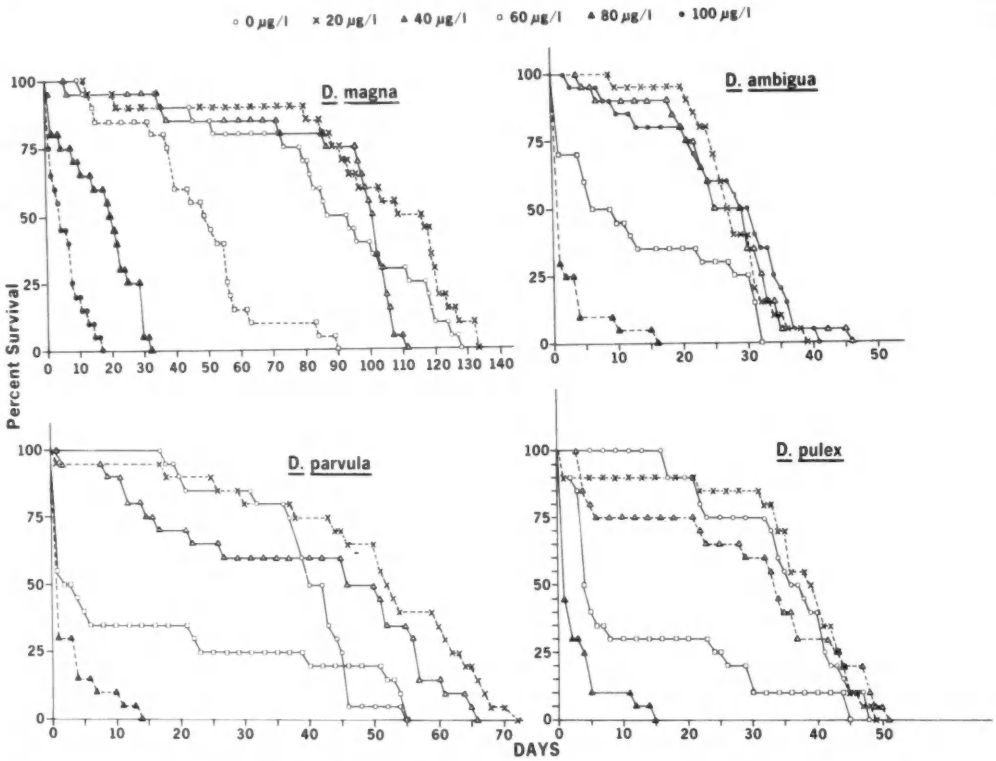

FIG. 1. Survivorship curves for four species of *Daphnia* subjected to chronic copper exposures. Each curve is based on an initial cohort of 20 animals.

the die-off at 60 µg/liter did not begin until the experiment had progressed beyond day 30 (Fig. 1). Obviously, daphnids very rarely, or never, attain their physiological life expectancy in the real world, and one could speculate that it is really not worth the effort to carry chronic experiments through to the death of the last animal. It is clear, however, that *D. magna* was under stress at a copper concentration of 60 µg/liter and that this would not have been detected in a 3-wk chronic bioassay. Given the added stresses imposed on a species as a component of a more complicated community, a copper concentration of 60 µg/liter would possibly tip the scales sufficiently to eliminate the species. The problem of extrapolating from laboratory experiments to more complex, natural systems is the crucial problem. Sooner or later, if we want to protect species in complex communities, we shall have to study stressed animals as components of more complex systems.

EFFECT OF CHRONIC COPPER EXPOSURE ON MEAN BROOD SIZE

In daphnids not exposed to a toxic stress, reproductive performance is largely determined by temperature and food resources. Because these parameters were the same for all animals in the present study, differences in reproductive performance can be attributed to either genetic differences or to the effects of exposure to different copper concentrations. Since we are dealing with parthenogenetic reproduction, most of the variability can be attributed to the impact of the copper stress.

Reproductive output can be affected directly by a toxicant (causing a change in brood size or in frequency of reproduction) or, indirectly, by shortening the life span of the female (fewer broods) or changing the duration of reproductive maturation. Studies that do not entail frequent examination of individual animals do not provide

the investigator information which will allow discrimination between the direct and indirect effects of a toxicant on reproductive output. Our daily records show that copper did not delay reproductive maturation nor did it change the frequency of reproduction. Copper did, however, affect reproductive output indirectly by shortening the life span of the females or directly by causing an increase or decrease in brood size.

Reproductive response of the four species to a chronic copper stress was somewhat more variable than was survival. Temporal changes in mean brood size, at each copper concentration, are illustrated in Fig. 2 for the four species. Although brood sizes oscillate, there is no evidence that any of the species approached a reproductive senility in old age. The oscillatory pattern does suggest that results of an analysis of the impact of copper on brood size might vary according to when the analysis was made during the life span of the various cohorts.

Daphnia magna was, reproductively, relatively insensitive to copper in the pond-water algal system. At no time, from brood 1 through brood 33, was cumulative mean brood size at 80 μg/liter significantly smaller than that of control animals. Furthermore, copper was stimulatory up through a copper concentration of 60 μg/liter, i.e. mean brood sizes were larger than those of control animals and, almost always, significantly so. Conclusions as to the effect of copper on brood size would have been virtually the same no matter how long the experiment had been run. Total reproductive output of a cohort of *D. magna* decreased at copper concentrations greater than 40 μg/liter (Table 2) only because the adults had a shortened life span and therefore produced fewer broods.

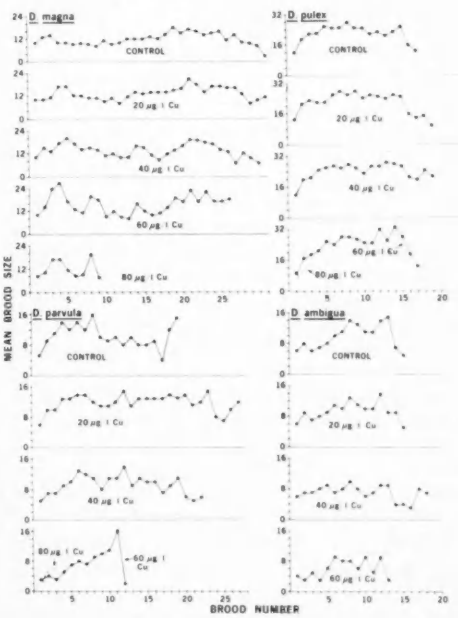

FIG. 2. Temporal changes in mean brood sizes of four species of *Daphnia* subjected to chronic copper exposures. Each curve is based on an initial cohort of 20 animals.

There were no significant differences in the mean brood sizes of *D. pulex* reared in 0, 20, 40, 60, and 80 μg Cu/liter for cumulative broods 1 and 2. Analyses of cumulative mean broods 3 through 19, however, agreed that mean brood sizes of animals maintained at 80 μg/liter were always significantly smaller than those of the other animals. Although mean brood size of animals reared at 20 and 40 μg Cu/liter were usually larger than those of control animals, the differences were never significant. The experiment could have been terminated any time after the third brood without altering conclusions as to the effect of copper on reproduction of *D. pulex*.

Daphnia parvula reared in 60 and 80 μg Cu/liter had mean brood sizes that were significantly smaller than those of control animals from cumulative broods 1 through 8. Mean brood sizes were not significantly different for animals reared at 0, 20, and 40 μg/liter. When cumulative mean brood sizes were analyzed subsequent to brood 8, only animals maintained at 80 μg Cu/liter had mean brood sizes significantly smaller than those of control animals and there were no significant differences between animals cultured at 0, 20, 40, and 60 μg Cu/liter. For *D. parvula*, therefore, stopping the experiment prior to the production of the ninth brood would have indicated a greater reproductive sensitivity than would have been indicated if the experiment had been carried beyond brood 9.

If analyzed prior to cumulative brood 10, mean brood sizes of *D. ambigua* were significantly reduced only in copper concentrations of 60 μg/liter. Analyses of cumulative mean broods 10 through 18, indicate that animals reared in copper concentrations of 40 and 60 μg/liter had mean brood sizes significantly smaller than animals reared at 0 and 20 μg/liter. There was no reproduction in copper concentrations 60 μg/liter, and copper did not cause a significant increase in mean brood sizes of *D. ambigua* at any time during the experiment.

In summary, *D. magna* was least sensitive,

TABLE 3. Instantaneous rate of population growth (r) as affected by copper for four species of *Daphnia*. Horizontal lines indicate that the r-values above and below the line are significantly different ($P \leq 0.05$) as determined by Duncan's new multiple range test (Duncan 1955).

Cu (μg/liter)	*D. magna*	*D. pulex*	*D. parvula*	*D. ambigua*
0	0.373	0.498	0.423	0.459
20	0.405	0.469	0.424	0.454
40	0.409	0.453	0.390	0.432
60	0.325	0.230	—[a]	0.233
80	0.287	—[a]	—[a]	—[a]
100	—[a]	—[a]	—[a]	—[a]

[a]No reproduction occurred at these concentrations.

reproductively, to a chronic copper stress. It was the only species in which copper stimulated reproduction and in which there was no significant reduction in brood sizes at any copper concentration. *Daphnia pulex* was the second least sensitive to copper; only at a copper concentration of 80 μg/liter was there a significant reduction in mean brood size. *Daphnia parvula* was the third least sensitive; if analyzed prior to brood 9 there was a significant reduction in mean brood size in a copper concentration of greater than 60 μg/liter. *Daphnia ambigua* was the most sensitive; mean brood sizes were at all times significantly smaller in 60 μg/liter and, if analyzed after brood 9, mean brood sizes were significantly reduced in 40 μg/liter.

Effect of a Chronic Exposure on the Instantaneous Rate of Population Growth (r)

The statistic, r, takes into account longevity and all facets of reproduction (e.g. age at reproductive maturity, age at reproductive senility, frequency of reproduction, and number of offspring per brood). Although other stresses may have different effects, in the present study, r-values within a species were largely determined by the interaction between longevity and brood size. Differences between species, however, were also related to species differences in frequency of reproduction and age at reproductive maturity.

Species differences in r are presented in Table 3. *Daphnia magna* had the smallest r-values under control conditions. This is a reflection of: 1) longer maturation time (*D. magna* produce their first young at an age of about 7 days, *D. pulex* at an age of 6 days, *D. parvula* and *D. ambigua* at an age of 5 days); 2) longer period of embryological development (3 days for *D. magna* and 2 days for the other species); and 3) *D. pulex* had larger broods than did *D. magna* (Fig. 2). The early maturation and short period of embryological development of *D. ambigua* was somewhat negated by its producing the smallest broods of any of the four species (Fig. 2).

Table 3 shows that, except for *D. magna*, there is a significant reduction in r at concentrations of copper > 40 μg/liter. In the three smaller species this is due to an increase in mortality and a reduction in brood size. In fact, reproduction is shut-off completely for the three smaller species at a copper concentration of 80 μg/liter.

Comparison of Longevity, Brood Size, and r as Indices of Copper Stress

Longevity and r both predict that the three smaller species would be adversely affected at copper concentrations greater than 40 μg/liter (Fig. 1 and 2). For *D. magna*, however, longevity is a more sensitive index than is r (Fig. 1 and Table 3). This reflects the stimulatory effect of copper on brood size in *D. magna*, which more than offsets the reduced longevities at 60 μg/liter. In *D. magna*, *D. pulex*, and *D. parvula*, brood size is less sensitive to a copper stress than either r or longevity. For *D. magna*, use of brood size as an index would suggest an allowable copper concentration twice that predicted for longevity. For *D. ambigua*, the three indices are in agreement in predicting that the species would be adversely affected at copper concentrations > 40 μg/liter.

Evaluation of the Application-Factor Concept

Application factors were calculated using only those LC50 values from parallel dose–response curves (Table 1), and the maximum acceptable toxicant concentration (MATC) was calculated from the chi-square analyses of combined survivorship curves for two chronic tests for each species. Survivorship was used as the estimate of

MATC because it was as, or more, sensitive than brood size or r for each of the four species. These application factors are: 0.59 for *D. ambigua*, 0.56 for *D. parvula*, 0.47 for *D. pulex*, and 0.47 for *D. magna*.

We can find no references in the literature to application factors for *Daphnia*. Copper application factors, as reported in the literature for fish, are much smaller than those we have observed for *Daphnia*. For example, in a study of brook trout (*Salvelinus fontinalis*), the application factor for copper was estimated to lie between 0.10 and 0.17 (McKim and Benoit 1971). Mount (1968) and Mount and Stephan (1969), working with fathead minnows (*Pimephales promelas*), estimated the application factor for copper to be between 0.03 and 0.07 in hard water and between 0.14 and 0.24 in soft water. The larger application factors for the daphnids may be due to the fact that an acute test comprises a much greater fraction of the total life cycle of daphnids than of the life cycle of fishes.

Conclusions

Survival is the best index of a copper stress since it was as, or more, sensitive than any of the other indices and also was the least variable. If a decrease in survival is used as the index, the four species of *Daphnia* do not differ in their sensitivity to a copper stress, and factors, other than sensitivity to copper, would dictate which species should be used in bioassays. *D. magna* is easier to handle because of its larger size. If generation-length chronic bioassays are to be conducted, however, the shorter generation times of the smaller species are advantageous. The generation times for *D. parvula* or *D. pulex* were only about ⅓ that of *D. magna* and that of *D. ambigua* only about ¼. If chronic bioassays are to be run for less than a generation, the smaller species should be utilized since the effect of the stress on longevity becomes apparent more quickly than it does for *D. magna*.

If the four species tested are representative of the genus, an application factor calculated for one species should protect other species within the genus under similar physicochemical conditions. It remains to be seen whether or not this will prove true for other toxicants.

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DDT Residues in Benthic Invertebrates and Demersal Fish in St. Margaret's Bay, Nova Scotia[1]

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HARGRAVE, B. T., AND G. A. PHILLIPS. 1976. DDT residues in benthic invertebrates and demersal fish in St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 33: 1692–1698.

Organochlorine residues (*p,p'*-DDT and its metabolites) were measured in samples of benthic invertebrates and demersal fish taken from St. Margaret's Bay, Nova Scotia. No other organochlorine compounds were present in detectable amounts. ΣDDT levels in whole organisms, excluding lipid-rich tissues, grouped as benthic epifauna, infauna, and demersal fish were not significantly different and thus no accumulation occurs in this food chain. Atmospheric supply is probably the major source of low levels of contamination and a detritus-based food web may equalize residue concentration between various feeding types.

HARGRAVE, B. T., AND G. A. PHILLIPS. 1976. DDT residues in benthic invertebrates and demersal fish in St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 33: 1692–1698.

Nous avons mesuré les résidus organochlorés (*p,p'*-DDT et ses métabolites) dans des échantillons d'invertébrés benthiques et de poissons démersaux capturés dans la baie St. Margaret, Nouvelle-Écosse. Aucun autre pesticide ou composé organochloré ne sont présents en quantités détectables. Les niveaux de DDT total dans les organismes entiers, à l'exclusion des tissus riches en lipides, groupés en épifaune benthique, endofaune et poissons démersaux, ne different pas de façon significative. Il n'y a donc pas accumulation dans cette chaine alimentaire. L'apport atmosphérique est probablement la source majeure de bas niveaux de contamination, et un réseau alimentaire basé sur les détritus peut égaliser la concentration des résidus entre les organismes ayant divers types d'alimentation.

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A survey during 1973 in St. Margaret's Bay, N.S., was intended to quantify organochlorine residue concentrations in various groups of benthic organisms in an area remote from immediate pesticide release. While the level of organochlorine residues in any organism is a static index of a dynamic process (Kerr and Vass 1973), it identifies the presence and relative amounts of particular compounds. Measurable residue concentrations in benthos in St. Margaret's Bay, an area not subject to direct application of the material, implicate atmospheric translocation as a source of supply. A comparison of residue levels in predator and prey organisms in such an environment could establish present-day background levels typical of unpolluted coastal marine waters and indicate those animals most susceptible to accumulation through food chain transfer.

Materials and Methods

Samples of benthic invertebrates and demersal fish were obtained from the deep central (60–75 m) and littoral (5–20 m) areas of St. Margaret's Bay during April and May 1973. Van Veen (0.1 m^2) bottom grabs were taken from an anchored boat and fauna was collected as described by Peer (1970). A small otter trawl towed at 2 knots was used to collect demersal fish species. All organisms were placed in glass jars or vials within 3 h of collection and held at −20 C until analyzed. Containers were pre-rinsed with hexane and acetone and similarly rinsed aluminum foil was used to line caps to prevent contamination.

Organochlorine residues present in groups of benthic invertebrates sorted to species in whole fish and dissected tissues, were measured. Small invertebrates were grouped to provide a sample size at least 1 g wet wt. Extractions were carried out by homogenizing each sample for 2 min in a blender with a stainless steel chamber containing a chloroform: methanol (2:1) solvent mixture described by Folch et al. (1957) but used in a slightly modified procedure (Sameoto et al. 1975). The chloroform phase of the extracts was reduced in volume by gentle

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rotary evaporation, taken up in n-hexane, and reduced to a small volume to remove chloroform. Aliquots of this solution were placed in preweighed aluminum foil cups and dried to a constant weight (24-h) over silica gel in a desiccator. Weights of material in this extract, taken as equivalent to lipid content, were expressed as a percentage of original wet tissue weight. The presence of *p,p'*-DDT[2] was confirmed through saponification (reflux of residue with 2.5% alcoholic KOH for 15 min at 40 C) and conversion to *p,p'*-DDE (Holden and Marsden 1967). All determinations were carried out in duplicate, and average values were calculated.

Recovery of ^{3}H-*p,p'*-DDT, "spiked" into various types of sample material to serve as an internal standard, ranged from 78 to 90%. No correction for loss during extraction and subsequent analysis by gas–liquid chromatography has been applied to estimates of residue concentrations. The analytical procedure has been described by Addison et al. (1972).

Results

Three DDT related compounds (*p'p,*-DDE, *p,p'*-DDT, and *p,p'*-DDD) were present in sufficient quantities for reliable determination (Table 1). No peak corresponding to *o,p*-DDT or dieldrin (detected in a 15% ether–hexane eluate from Florisil) (Addison et al. 1972) was observed in any sample. Also, peaks attributable to PCB's, some of which have a column retention time similar to that of *p,p'*-DDD and *p,p'*-DDT (Addison et al. 1972) were absent.

Residues of *p,p'*DDE, present in all tissues and organisms examined, ranged in concentration from 1 ppb wet wt in whole mussels and amphipods to over 1000 ppb wet wt in liver samples from the skate *Raja radiata*. Residues of *p,p'*-DDT were not found in every sample and when present, concentrations were usually equal to or less than those of *p,p'*-DDE. Exceptions to this trend, however, included various infaunal species and the mussel *Mytilus edulis*. The *p,p'*-DDD metabolite was observed only in *M. edulis*, in Atlantic cod (*Gadus morhua*) and skate liver samples, and in the carcass of one large American plaice (*Hippoglossoides platessoides*). Peaks which chromatographically corresponded to *p,p'*-DDD were observed in some other samples but these were too small for reliable measurement.

The relative proportions of the metabolites to the parent pesticide may be regarded as an index of metabolism of *p,p'*-DDT by organisms. In several mammals *p,p'*-DDE is the principal storage metabolite of the DDT group, and its concentration relative to ΣDDT (*p,p'*-DDT, *p,p'*-DDE, and *p,p'*-DDD) residue present, may serve to indicate metabolic degradation which has occurred. Levels of *p,p'*-DDE expressed as a percentage of ΣDDT present varied considerably in different organisms but the values tended to fall into two broad groups. Less than 50% of the ΣDDT residue in benthic invertebrates (snails, holothurians, cumaceans, mussels, and four species of infauna) was *p,p'*-DDE. In all species of demersal fish, predatory starfish, and gastropods (*Thais lapillus*) 75% of the ΣDDT residue was *p,p'*-DDE. One exception to this division were the amphipods, *Ampelisca* spp. Only *p,p'*-DDE was detected in these organisms and concentrations were the lowest observed (Table 1). Since the limit of reliable detection was 1 ppb, other metabolites of DDT could have been present in lower concentrations which would not have been detected.

ΣDDT levels in whole organisms, excluding lipid-rich tissues, grouped as benthic epifauna, infauna, or demersal fish (Table 1) were not significantly different (means: 9.8, 13.8, 10.8 ppb wet wt, respectively) by a modified Duncan's multiple range test for group means with unequal numbers (Kramer 1956). Thus, on a wet tissue basis, no accumulation of *p,p'*-DDT or its metabolites occurs in demersal fish feeding on benthic invertebrates in St. Margaret's Bay. Also, although some individual samples contained ΣDDT concentrations significantly higher (snails, lobsters, Lumbrinerid polychaetes, and plaice) and lower (amphipods and mussels) than mean levels, the differences were not great and they were unrelated to feeding habits or body size.

The hydrophobic nature of organochlorine compounds tends to concentrate residues in fatty tissues. Expression of residue levels on the basis of concentration per unit lipid weight thus provides a standardized basis for comparison. Storage organs rich in lipids contain the highest levels of DDT residues observed in samples from St. Margaret's Bay. Concentrations in lobster hepatopancreas (9–13 ppm) were an order of magnitude higher than those present in cod liver (0.7–2.8 ppm) and more than twice those in skate liver (4.6 ppm). Lipids in all other organisms contained between 0.05 and 2.5 ppm ΣDDT residues.

Maximum ΣDDT concentrations on a lipid basis for whole organisms were found in lobster, cod, and plaice muscle and in benthic Lumbrinerid polychaetes and the mollusc (*Crenella glandula*) (Table 1). Other benthic invertebrates (amphipods, *M. edulis*, *Littorina littorea*) contained the

[2]Abbreviations used: *p,p'*-DDT(2,2-bis-*p*-chlorophenyl-1,1,11-trichloroethane); *p,p'*-DDE(2,2-bis-*p*-chlorophenyl-1,1-di-chloroethylene); *p,p'*-DDD(2,2-bis-*p*-chlorophenyl-1,1-di-chloroethane).

TABLE 1. Organochlorine residue concentrations and lipid content of invertebrates and demersal fish from St. Margaret's Bay collected April–May 1973. Each value is the mean of at least two replicate analyses of one sample. Lipid concentration is expressed as a percentage of wet weight. Minimum level of reliable detection equivalent to 1 ppb = 1 ng/g.

Sample	Size (*mm*)	No. of animals	% Lipid	Wet tissue (*ppb*)				Lipid fraction (*ppb*)			
				p,p'-DDE	*p,p'*-DDT	*p,p'*DDD	ΣDDT	*p,p'*-DDE	*p,p'*-DDT	*p,p'*-DDD	ΣDDT
						Epibenthos					
Littorina littorea (Gasteropoda)	27	1	8.87	9.6	10.8	—	20.4	108.2	121.7	—	230
	18–19	6	5.29	9.9	—	—	9.9	187.1	—	—	187
	15–17	9	5.89	6.3	—	—	6.3	107.0	—	—	107
	12–14	19	4.40	4.2	—	—	4.2	95.5	—	—	96
	12–14	17	4.58	5.3	—	—	5.3	115.7	—	—	116
	9–11	12	10.17	13.0	—	—	13.0	127.8	—	—	128
	5–8	10	3.48	29.3	—	—	29.3	842.0	—	—	842
Thais lapillus (Gasteropoda)	17–20	23	3.78	9.3	—	—	9.3	246.0	—	—	246
	21–24	11	3.14	12.6	—	—	12.6	401.3	—	—	401
Ampelisca spp. (Amphipoda)	2–5	35	2.28	1.2	—	—	1.2	52.6	—	—	53
Psolus phantapus (Holothuria)	100	1	1.59	1.5	1.6	—	3.1	94.3	100.6	—	195
Asterias vulgaris (Echinodermata)	100	5 (gonads)	3.60	9.6	2.9	—	13.0	266.7	80.6	—	347
Eudorella spp. (Cumacea)	2	30	2.31	8.0	9.0	—	17.0	346.3	389.6	—	736
Homarus americanus (Decapoda)											
Muscle	400	1	0.76	24.0	—	—	24.0	3157.9	—	—	3158
	250	2	0.70	11.0	—	—	11.0	1571.4	—	—	1571
Hepatopancreas	400	1	7.13	940	—	—	940	13183	—	—	13183
	250	2	4.22	400	—	—	400	9479	—	—	9479
Mytilus edulis (Pelecypoda)	10	4	1.05	—	—	0.4	0.4	—	—	38.1	38
	25	3	1.14	1.3	7.3	8.6	—	114.0	640.4	—	754
	40	2	2.90	3.0	3.8	3.3	10.1	103.4	131.0	113.8	348
	60	3	2.39	1.8	2.4	2.1	6.3	75.3	100.4	87.9	264
	70	4	2.45	2.5	3.2	2.8	8.5	102.0	130.6	114.3	347
	96	1	2.67	2.7	3.8	2.9	9.4	101.7	142.3	108.6	353
	99	1	1.85	2.2	3.0	2.3	7.5	118.9	162.2	124.3	405
Modiolus modiolus (Pelecypoda)	90	2	1.49	3.0	—	—	3.0	201.3	—	—	201
	125	1	1.80	1.0	1.4	—	2.4	55.5	77.8	—	133

TABLE 1 (*Concluded*)

Sample	Size (*mm*)	No. of animals	% Lipid	Wet tissue (*ppb*)				Lipid fraction (*ppb*)			
				p,p'-DDE	*p,p'*-DDT	*p,p'*DDD	ΣDDT	*p,p'*-DDE	*p,p'*-DDT	*p,p'*-DDD	ΣDDT
						Benthic infauna					
Glycera capitata	55	4	3.12	5.0	6.0	—	11.0	160.3	192.3	—	353
Lumbrineris spp.	35	10	2.17	5.0	19.0	—	24.0	230.4	875.6	—	1106
Clymenalla torquata	40	16	1.47	3.0	5.0	—	8.0	204.1	340.1	—	544
Crenella glandula	3	25	0.63	4.0	8.0	—	12.0	634.9	1269.8	—	1905
						Demersal fish					
Gadus morhua (Atlantic cod)	carcass	2	1.51	5.0	—	—	5.0	331.1	—	—	331
			0.55	8.0	3.0	—	11.0	1454.5	545.5	—	2000
	muscle	2	0.67	4.0	5.0	—	9.0	597.0	746.3	—	1343
	350		1.33								
			31.8	830.0	22.0	33.0	885.0	2610.1	69.2	103.8	2783
	liver	3	32.8	600.0	30.0	—	630.0	1829.3	91.5	—	1921
			40.8	299.0	—	—	299.0	732.8	—	—	733
Pseudopleuronectes americanus (Winter flounder)	muscle		1.37	2.0	—	—	2.0	146.0	—	—	146
	carcass	4	2.41	4.0	—	—	4.0	166.0	—	—	166
	230										
	gonad		5.13	9.0	—	—	9.0	175.4	—	—	175
Hippoglossoides platessoides (American plaice)	150 (90 g)	Whole	1.31	23.3/11.1	7.0/5.0	—	23.2	1771/847.3	5344/381.7	—	1767
	165 (120 g)	Whole	1.76	14.0	—	—	14.0	795.5	—	—	796
	200 (150 g)	Whole	1.78	40.1/27.2	16.1/11.5	—	47.5	2253/1528	904.5/646.1	—	2666
	320 (500 g)	Muscle	.72	10.0/2.1	2.0/1.0	—	7.5	1388.9/291.7	277.8/138.9	—	1153
	320 (500 g)	Carcass	.95	10.5/10.0	3.1/2.1	3.0	15.9	1105.3/1052.6	326.3/221.1	315.8	1669
Melanogrammus aeglefins (Haddock)	350	Muscle	.96	6.5	—	—	6.5	677.1	—	—	677
		Carcass	1.23	0.8	—	—	0.8	65.0	—	—	65
		Liver	29.2	72.3	—	—	72.3	247.6	—	—	248
Raja radiata (Thorny skate)	675	Muscle	.76	2.2	3.1	—	5.3	289.5	407.9	—	697
		Liver	51.8	1850/1090	580/620	330/390	2430	3560/2020	1120/1140	640/730	4605
Anarchichas lupus (Atlantic wolffish)	450	1 Muscle	1.10	6.3	—	—	6.3	572.7	—	—	573
		1 Muscle	2.33	13.7	—	—	13.7	588.0	—	—	588

lowest concentrations observed. ΣDDT concentrations in American flounder (*Pseudopleuronectes americanus*) and haddock (*Melanogrammus aeglefinus*) tissues were only slightly higher than those in these invertebrates. Additional evidence for lack of accumulation of *p,p'*-DDT and its metabolites in this benthic food chain exists in the low concentrations in invertebrate species known to be carnivorous. The gastropod *T. lapillus* and the polychaete *Glycera capitata* contained ΣDDT concentrations equal to or less than their probable prey (other benthic infauna). In addition, large carnivorous fish (thorny skate, *R. radiata*) and Atlantic wolffish (*Anarhichas lupus*) contained relatively low ΣDDT residues despite their supposedly high trophic position.

No consistent trend in lipid concentration, excluding storage organs, existed between faunal groups, although large organisms of a single species (snails, mussels, plaice) tended to have slightly higher lipid content. The tendency for some organisms to have higher ΣDDT residues on a lipid basis, however, was not directly related to enhanced lipid content. Similarly, samples with a low lipid content (lobster, fish muscle, *C. glandula*) did not contain correspondingly low ΣDDT residues.

Discussion and Conclusions

ΣDDT concentrations in St. Margaret's Bay fauna are among the lowest recorded for species of marine fish and invertebrates. For example, concentrations of 10–20 ppb of ΣDDT in oyster tissue are considered as background levels of "negligible significance" (Butler 1966) and they approach minimum levels that can be reliably determined. Sprague and Duffy (1971) observed ΣDDT residues of 100 ppb or less in wet tissue as an average concentration in whole body or muscle of lobsters and various molluscs and fish from the Gulf of St. Lawrence and they consider these to be low relative to previous studies. ΣDDT concentrations in benthic invertebrates and demersal fish in St. Margaret's Bay are an order of magnitude below this level (grand mean 10.5 ± 8.8 ppb, wet tissue) and although the levels are higher than those observed in mixed zooplankton samples from the North and South Atlantic shelves and open ocean (Risebrough et al. 1972), they are similar to those found in euphausiid populations in the upper estuary of the Gulf of St. Lawrence (Sameoto et al. 1975).

Animals rich in lipid are usually observed to contain higher organochlorine residue levels and often a direct positive correlation between total lipid content and residue burden is observed (Earnest and Benville 1971). Sprague and Duffy (1971) did not measure lipid content, but salmon, cod, and hake viscera contained 6–15 times higher concentrations of ΣDDT than did muscle. Mackerel, an oil-rich fish, contained 4–5 times ΣDDT concentrations observed in other fish. Similar relatively high ΣDDT concentrations in storage organs (lobster hepatopancreas, liver of fish species, Table 1) were observed in the present study. Liver samples from the thorny skate (*R. radiata*) contained the most lipid (51.8%) and the highest ΣDDT concentrations (4.6 ppm, lipid wt). Whole organisms and muscle tissue, however, did not contain ΣDDT residues in proportion to their lipid.

Numerous factors contribute to variation of organochlorine residue levels in single species (Addison et al. 1972), but it is worthwhile to compare general concentrations in lipids of various marine organisms representative of broad geographical areas which have not received direct application of DDT. Such a comparison, if representative of minimal concentrations, might indicate present day background residue levels which have resulted from atmospheric input and other forms of translocation such as animal migration. Cohen and Pinkerton (1966) and Södergren (1972) have discussed analyses of rainwater and dust which demonstrate dispersal of organochlorine compounds through the atmosphere.

A preliminary collation of some published estimates of ΣDDT levels in marine organisms from areas not subjected to direct input of organochlorine compounds indicates a range of values from 10 to 5000 ppb (Fig. 1). Ranges are somewhat misleading, however, since over 70% of the observations lie between 100 and 1000 ppb ΣDDT (lipid wt). While single high values distort such comparisons, averages do not adequately represent the range or variation in ΣDDT concentrations. Data from diverse geographic

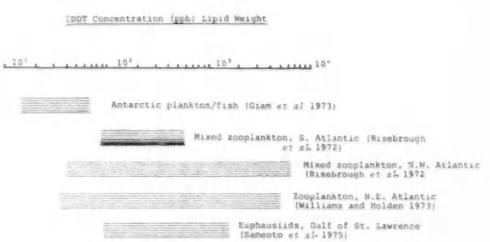
ΣDDT Concentration (ppb) Lipid Weight
10¹
10²
10³
10⁴
Antarctic plankton/fish (Giam et al 1973)
Mixed zooplankton, S. Atlantic (Risebrough et al. 1972)
Mixed zooplankton, N.W. Atlantic (Risebrough et al. 1972
Zooplankton, N.E. Atlantic (Williams and Holden 1973)
Euphausiids, Gulf of St. Lawrence (Sameoto et al. 1975)
Demersal fish/benthic invertebrates St. Margaret's Bay (present study)

FIG. 1. Comparison of ΣDDT concentration in lipid of marine organisms collected from areas not receiving direct input of organochlorine compounds.

locations do indicate, however, a relative uniformity in total DDT residue levels in widely separated marine habitats. Kerr and Vass (1973) and many previous authors have reached similar conclusions — namely that DDT-related residues are chronic contaminants present throughout the biosphere. What has been established from the data discussed here, however, is that a minimum level of contamination may exist, which can be considered a background level, in all marine food chains.

The resistance of organochlorine compounds to metabolic degradation, which is the reason for their persistence, is well known. It is generally accepted that *p,p'*-DDT is metabolized to *p,p'*-DDD and *p,p'*-DDE (MacGregor 1974) but where this occurs is uncertain. Darrow and Addison (1973) have shown that *p,p'*-DDT is neither metabolized nor excreted by the thorny skate (*R. radiata*) during 3 wk and experiments with zooplankton (*Calanus finmarchicus*) indicate a similar lack of metabolic conversion over an 8-wk exposure below 6 C (Darrow and Harding 1975). Photochemical degradation at the air–sea surface or bacterial decomposition of DDT-related compounds adsorbed to suspended and sedimented particulate matter may be important for the conversion. Whatever the pathways, the major metabolite, *p,p'*-DDE, undergoes little further degradation and it is usually this compound that accumulates with increasing age in organisms (Addison et al. 1973, MacGregor 1974).

The presence of *p,p'*-DDE in samples from St. Margaret's Bay indicates that degradation of *p,p'*-DDT has occurred either externally before incorporation, or within the tissues of organisms. While the site of metabolic conversion cannot be identified, it is significant that filter-feeding molluscs and snails feeding on attached epiphytic material and seaweed debris contained proportionately higher amounts of *p,p'*-DDT than did other organisms. The presence of higher concentrations of *p,p'*-DDT than its metabolites in molluscs suggests that the food supply (suspended and sedimented particulate material) of these organisms may serve as the route of entry of *p,p'*-DDT to the food chain. Absence of detectable amounts of *p,p'*-DDE and *p,p'*-DDD and the presence of *p,p'*-DDT ($<$ 1 ppb fresh wt, 10 ppm, lipid wt) in zooplankton in St. Margaret's Bay (Darrow and Harding 1975) supports the idea that undegraded pesticide is present in suspended particulate matter. Presumably supply is by atmospheric input and residues are recycled within the system in particulate form.

The relative importance of dissolved and particulate (ingestion) pathways of accumulation of organochlorine residues by aquatic organisms has been discussed in numerous studies (Kerr and Vass 1973). While opinions differ, it is generally agreed that the marked affinity of hydrophobic compounds like DDT for particulate substrates reduces availability for direct uptake. Food chain transfer is thus an important source of residues in aquatic organisms.

The apparent lack of food chain accumulation in the present data set may be attributable to the organisms considered and the low residue levels involved. Low concentrations may represent steady state conditions resulting from a small chronic atmospheric supply of *p,p'*-DDT with constant recycling. Excretion by organisms, adsorption on particulate matter, and subsequent re-ingestion by filter- and detritus-feeding invertebrates and predators, would equalize concentrations within various feeding types. A slow continual accumulation in storage organs of the largest and longest-lived organisms as observed would be expected.

This view of organochlorine cycling is consistent with Isaacs' (1972, 1973) ideas concerning the effect of food chain structure (simple, linear vs. complex, web) on the potential distribution of pollutants in aquatic organisms. Less accumulation of cesium in fish tissue was observed in a complex food web than in a more structured food chain where the same species were thought to have a more limited spectrum of food organisms. Thus, a catholic diet is viewed as conferring many alternative pathways for material and energy flow which results in a more homogeneous distribution of recycled and accumulated material.

Most sublittoral benthic communities are fueled largely by transfer of energy and material through detritus-based food chains. It has long been realized that a food web more realistically describes nutritional interactions between bottom organisms than does a concept of linear transfer through successive trophic levels. Detritus may also be an important food source for organisms in pelagic ecosystems and even planktonic food chains may be detritus-based to a large degree (Pomeroy 1974).

As the present study demonstrates, organisms of comparable life span, and thus storage potential, in such food webs will tend to contain a more homogeneous distribution of trace substances than would be expected on the basis of concentration at each step of food chain transfer.

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Taxonomy and Biology of Some Newfoundland Marine Leeches (Rhynchobdellae: Piscicolidae)

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KHAN, R. A., AND M. C. MEYER. 1976. Taxonomy and biology of some Newfoundland marine leeches (Rhynchobdellae: Piscicolidae). J. Fish. Res. Board Can. 33: 1699–1714.

Taxonomy and biology of 4 species of marine Piscicolidae belonging to the *Malmiana–Oceanobdella* complex were studied on the coast of Newfoundland from 1970 through 1974. Species include *Malmiana brunnea*, *M. scorpii*, and *Oceanobdella microstoma*, which infest shorthorn (*Myoxocephalus scorpius*) and longhorn sculpin (*M. octodecemspinosus*) and *O. sexoculata*, which occurs in the buccal cavity of ocean pout (*Macrozoarces americanus*). Laboratory studies included host proclivity, mating, deposition and hatching of cocoons, and growth of the progeny. *Malmiana brunnea* and *M. scorpii* have the potential of producing 2 generations each year, but the life cycle in nature is probably annual: the young emerge in July through September, mature and breed in the spring of the next year, and die by midsummer following cocoon deposition. Life cycles of *O. microstoma* and *O. sexoculata* are also annual. Although cocoons of *O. sexoculata* hatch in August, young of *O. microstoma* do not emerge until late November. Young of both species mature the following spring, deposit cocoons, and die. Cocoons of *M. brunnea* and *M. scorpii* each contain an average of 3 and 5 eggs, respectively, but those of *O. microstoma* and *O. sexoculata* contain only 1 egg.

Malmiana nuda Richardson, 1970 and *Platybdella buccalis* Nigrelli, 1946 are considered junior synonyms of *M. brunnea* (Johansson, 1896) and *Oceanobdella sexoculata* (Malm, 1863), respectively.

KHAN, R. A., AND M. C. MEYER. 1976. Taxonomy and biology of some Newfoundland marine leeches (Rhynchobdellae: Piscicolidae). J. Fish. Res. Board Can. 33: 1699–1714.

De 1970 à la fin de 1974, nous avons étudié sur la côte de Terre-Neuve la taxonomie et la biologie de 4 espèces de Piscicolidae de mer appartenant au complexe *Malmiana–Oceanobdella*. Ces espèces sont *Malmiana brunnea*, *M. scorpii*, et *Oceanobdella microstoma*, qui infestent les chaboisseaux à épines courtes (*Myoxocephalus scorpius* et les chaboisseaux à épines longues (*M. octodecemspinosus*), et *O. sexoculata*, qui se rencontre dans la cavité buccale de la loquette d'Amérique (*Macrozoarces americanus*). Au laboratoire on a étudié, entre autres, le penchant pour l'hôte, l'accouplement, la déposition et l'éclosion des cocons, et la croissance de la progéniture. *Malmiana brunnea* et *M. scorpii* peuvent produire 2 générations par année, mais le cycle biologique dans la nature est probablement annuel: les jeunes émergent de juillet à la fin de septembre, atteignent la maturité et se reproduisent au printemps de l'année suivante, pour mourir vers le milieu de l'été après la déposition des cocons. Le cycle biologique de *O. microstoma* et de *O. sexoculata* est également annuel. Alors que les cocons de *O. sexoculata* éclosent en août, les jeunes de *O. microstoma* n'émergent pas avant la fin de novembre. Les jeunes des deux espèces atteignent leur maturité au printemps suivant, déposent leurs cocons et meurent. Les cocons de *M. brunnea* et de *M. scorpii* contiennent chacun en moyenne 3 et 5 œufs respectivement, mais ceux de *O. microstoma* et de *O. sexoculata* ne contiennent que l'œuf.

Malmiana nuda Richardson, 1970 et *Platybdella buccalis* Nigrelli, 1946 sont considérés comme des synonymes moins anciens de *M. brunnea* (Johansson, 1896) et *Oceanobdella sexoculata* (Malm, 1863), respectivement.

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THIS paper deals with 4 species of marine Piscicolidae belonging to the *Malmiana–Oceanobdella* complex, from the northwestern North Atlantic, in the vicinity of St. John's, Newfoundland. They include *Malmiana brunnea* (Johansson, 1896), *M. scorpii* (Malm, 1863), *Oceanobdella microstoma* (Johansson, 1896), and *O. sexoculata* (Malm, 1863). Except for *O. sexoculata*, which occurs in the mouth of ocean pout (*Macrozoarces americanus*), the other 3 species are characteristic leeches of the sculpins *Myoxocephalus scorpius*

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and *M. octodecemspinosus*, which henceforth are usually referred to as shorthorns and longhorns, respectively.

The foundations of marine Piscicolidae taxonomy were laid down by Johansson (1896, 1898, 1899) and Malm (1863, 1865, 1874), based chiefly on live material from Sweden and Greenland, and Selensky (1915). Except for Vasileyev (1939), Moore and Meyer (1951), and Richardson (1970), subsequent publications dealing with these leeches have been essentially limited to locality data and host records (Bayliss 1922; Bruun 1928, 1938; Epshtein 1961, 1962; Lütken 1875; Polyanskii 1955; Remy 1928; Vanhöffen 1897; Wesenberg-Lund 1926).

Preserved leeches in general and Piscicolidae in particular are not easily identified, and the validity of named species is often questioned. Piscicolidae present special problems because with preservation they lose their normal color and body proportions, and darken and harden in time; they are seldom available in adequate numbers, for their occurrence is dependent upon capturing their host(s); and they are often taken incidental to other studies, so that they are rarely subjected to proper killing and fixation methods.

In view of the problems involved in maintaining leeches and their hosts in the laboratory, under conditions simulating those in nature, it is not surprising that literature concerned directly with the ecology and behavior of Piscicolidae is scant. Some ecological information has been acquired, incidental to the basic collection data accompanying specimens and their description. Other valuable data, including fundamental details of life history and reproductive information, has come from maintaining the leech-infested hosts in the laboratory. Not more than a half dozen species have been studied ecologically.

Materials and Methods

Sculpins were collected by hook and line and by scuba divers, mainly from the Portugal Cove and Logy Bay areas near St. John's, at depths of 20–30 m. Divers reported that there was a disparity between the number of leeches present when a fish was collected and when it was examined again ashore. Leeches tended to leave the host with handling, and escaped through the fishnet bag used by the divers to hold the fish. Since only data obtained from the fish taken with hook and line are believed to be reliable, our infestation data are based only on fish taken this way. In the field examination of fish, the leeches were identified, counted and recorded as to host location, and placed in small glass jars containing sea water. After becoming familiar with the distinctive coloration of living specimens, with a little practice, one can easily make specific determinations macroscopically.

On returning to the laboratory, leeches were put with an adult sculpin in an aquarium (48 × 30 × 25 cm, with water flow rate of 1 liter/min), covered with netting to prevent escape of the fish and supplied with constantly flowing water; in cloth-covered 50 ml glass jars in running water; or leeches were anesthetized and fixed for examination. For growth studies leeches were removed from their host at 7–10-day intervals, anesthetized prior to measuring, and fixed. Also, stock populations of *Malmiana brunnea*, *M. scorpii*, and *Oceanobdella microstoma* were established on adult sculpins in 1969 and maintained throughout the study in concrete tanks (100 × 80 × 65 cm, with a water flow rate of approximately 5 liter/min). Temperature of the running water varied between −1 and 14 C, depending on the season. Ocean pouts were collected by divers and in trawls (80–210 m) on the Grand Banks, maintained alive in tanks aboard the *A.T. Cameron*, and examined for leeches at the Marine Sciences Research Laboratory, Logy Bay.

Leeches were studied alive and fixed, in serial sections, dissections, and as whole mounts. Before fixation leeches were anesthetized with 15% ethanol in sea water, cooled to 3 C. Following anesthetization, specimens were transferred to a slide and straightened, another slide added with supports to prevent flattening, and fixative (80% ethanol) added slowly. This resulted in straight, normally relaxed, and unflattened specimens.

Length measurements of leeches are overall, i.e. both suckers are included. Trachelosome and urosome refer to the parts of the body from the posterior edge of the clitellum forward and from the clitellum posteriorly, respectively. Measurements are based on 10 or more readings unless otherwise indicated. Synonymies are not intended to be exhaustive but are, rather, limited to the more important references which might be encountered. No attempt has been made to compile all occurrence records for each locality, as this would prove cumbersome and redundant; however, all original locality references are included.

Systematic Section

Malmiana Strand, 1942

Body rounded, skin pigmented and opaque, not, or only weakly, divided into trachelosome and urosome; no collar, tubercles, pulsatile vesicles, or other paired lateral structures; longitudinally streaked with brown or entirely brown. Both suckers large and well developed. Bursa small, when protruded forming only insignificant wart-like projection.

Malmiana brunnea (Johansson, 1896)

Abranchus brunneus Johansson, 1896: 32; *Ot-*

tonia brunnea; Johansson 1929: 140; *Malmiana brunnea*: Strand 1942: 398 [by implication]; *Ottonia brunnea*: Polyanskii 1955: 89; *Malmiana brunnea*: Epshtein 1962: 649; *Heptacyclus brunneus*: Epshtein 1967: 680; *Malmiana nuda* Richardson, 1970: 841.

Anatomy

Body rounded, normally not flattened; trachelosome not, or only slightly, narrower than urosome. Clitellum ditsinct, slightly narrower than rest of body. Body shape only slightly variable. Both suckers well developed. Anterior sucker cup-shaped at rest, directed somewhat downward, little wider than trachelosome; in active condition sucker much expanded. Up to 35 mm in length; widths of trachelosome and urosome, 1.2 and 1.5 mm, respectively; diameter of expanded oral and anal suckers, 1.3 and 1.5 mm, respectively.

In life basic body color brown, sometimes with somewhat reddish hue, slightly lighter ventrally; colorless transverse band, covering about 4 rings usually present in anal region. Some specimens with faint longitudinal striping: often with slightly lighter brown middorsal band, beginning on clitellum, widening slightly posteriorly, and continuing into the colorless banded anal zone; occasionally with additional light-colored pair of much narrower paramarginal stripes, one on each side, also beginning on the clitellum and continuing posteriorly to the colorless anal band (Fig. 3A). Young specimens without transverse banding characteristic of young *M. scorpii*. Entire body surface with numerous evenly scattered minute dark brown dots, visible after most of other pigment dissolved away (these dots are produced by pigment cells in the epidemis but, as pointed out by Johansson (1896: 56) they are skin glands filled with pigments, and are not to be confused with the pigment cells in the parenchyma and subepidermal connective tissue).

Complete segments basically 3-annulate, with each annulus further but less distinctly divided so that segments secondarily 6-annulate (Fig. 1). Secondary divisions clearer, more distinct in neural annulus (a2) and here the secondary annuli thus formed are slightly unequal (b3 > b4). Annulus a2 larger than either a1 or a3, both of which divide equally into secondary annuli. Complete segment formula is thus, (b1 + b2) < (b3 + b4) > (b5 + b6).

Three pairs of eyes present, all essentially crescent-shaped. Anterior pair, situated slightly postequatorially on oral sucker, have their crescents directed anterolaterally; second pair, slightly larger and closer together, face posterolaterally. Somewhat smaller crescents of third pair, on second ring and farther removed from second pair than is second pair from first pair, face forward and outward like first pair. One or both eyes of a pair may be altered in shape or divided. Abnormal eyes fairly common, but the loss of an eye (in living or recently preserved specimens) was not observed in *M. brunnea* or in any of the other 3 species.

Oral sucker colorless anteriorly, followed by

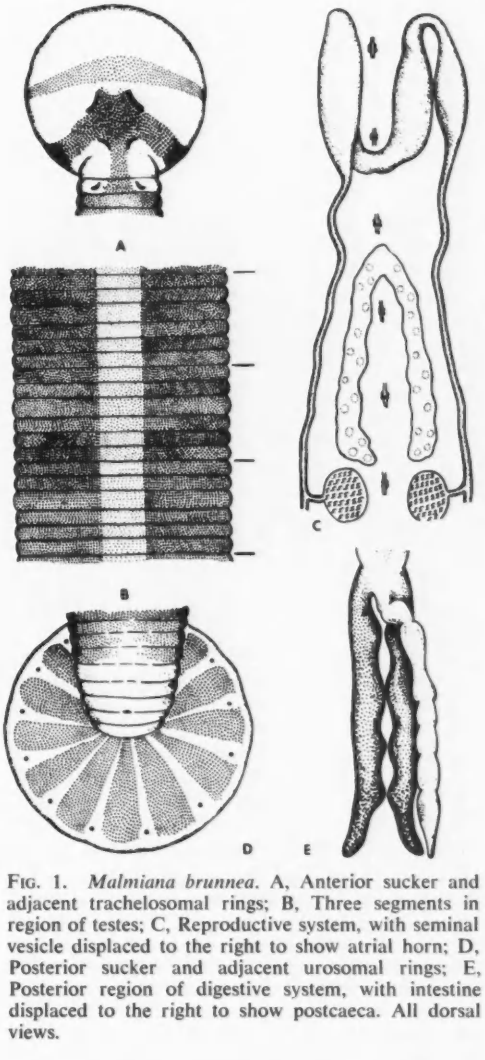

Fig. 1. *Malmiana brunnea*. A, Anterior sucker and adjacent trachelosomal rings; B, Three segments in region of testes; C, Reproductive system, with seminal vesicle displaced to the right to show atrial horn; D, Posterior sucker and adjacent urosomal rings; E, Posterior region of digestive system, with intestine displaced to the right to show postcaeca. All dorsal views.

2 brownish colored bars separated by a clear space. Foremost band crescent-shaped and lighter; second is wider, more banded and darker, with first and second pairs of eyes on fore and aft borders, respectively. Light-colored transverse band present in nuchal region. Middorsally, however, clear band interrupted by pigment from body that is confluent with rear band on anterior sucker.

Posterior sucker also cupped when at rest, little broader than urosome, with opening directed straight back or slightly downward; when extended, twice width of urosome. Sucker has brown center, with about 14 brown rays which diverge toward outer edge. Near periphery there is a circle of about 12 small ocelli, which alternate with diverging rays (the number of ocelli is variable and is of little value, if any, in separating this species from *M. scorpii*, the statement by Brunn (1928: 3) to the contrary notwithstanding).

Five pairs of testes in XIV/XV through XVIII/XIX, when fully developed, contiguous with one another. Vasa deferentia, capillary in testicular region, extend laterally along testes, increase slightly in diameter in XI and XII. Each of these expands in X and XI, forming seminal vesicle, the anterior end entering atrial horns (Fig. 1C). Cornua large, and unite to form short atrium, which opens at XI a2/a3. Bursa short, narrow, with very weak muscular wall; when everted, forms only small wart-like lump.

Ovaries paired simple sacs which, when filled with ova, extend to first testes or beyond. Sacs join anteriorly to form very small common oviduct, ending in female gonopore at XII a1/a2.

Proboscis, which opens slightly anterior to first pair of eyes, when at rest extends from anterior ganglionic mass back to between second and third free ganglia. Small esophageal ceca, first observed by Johansson (1896: 78), open in segment X. Stomach or crop consists of slightly constricted chambers in X through XIX, where it divides into muscular intestine and thin-walled postceca which extends to base of posterior sucker.

Muscular intestine wide and chambered: 2 large and several small inflations, followed by large thin-walled rectum, which opens 2 or 3 rings anterior to posterior sucker.

Postceca separate for their entire length, as pointed out by Johansson (1896: 70) and confirmed by Richardson (1970: 844). In some specimens postceca may appear fused, but they are functionally independent (Fig. 1E).

Occurrence

Sweden, Johansson (1896: 33); Greenland, Wesenberg-Lund (1926: 98); Bering Sea (Kamtchatka and Aleutian Isles), Vasileyev (1939: 57); White Sea, Shul'man and Shul'man, 1953 (according to Epshtein [1962: 649]); Barents Sea, Polyanskii (1955: 89); Massachusetts, Sawyer et al. (1975: 657).

A comparison of Richardson's description and types of *M. nuda* (nos. 42566 and 42567, 3 specimens in formalin) in the USNM Helm. Coll., with the detailed description of *Malmiana brunnea* (Johansson, 1896), pieced together from the author's illustrations and fragmentary statements, and similar data of Selensky (1915), leave no doubt that the 2 forms are conspecific.

The only distinguishing difference between them is that *M. nuda*, as the specific appellation suggests, lacks pigmentation. It is well known, as recently pointed out by Epshtein (1965: 1859; 1967: 1648), that pigments, including the melanin series of the eyes and ocelli, fade and may disappear completely with prolonged preservation of specimens. The fading process is hastened by strong light. While formalin is one of the best initial preservatives and is a widely used fixative, it suffers from the disadvantage of becoming extremely acidic with time and of rendering material unsatisfactory for use. The conclusion that Richardson's *M. nuda* is a blanched *M. brunnea*, with which it agrees internally, gains support from the fact that in none of the hundreds of *Malmiana brunnea* examined from the type locality and type host or any of the *M. scorpii* and *Oceanobdella microstoma*, all of which infest sculpins, were specimens found lacking the typical body coloration, eyes, and ocelli.

Biology

Host–parasite relationship — Malmiana brunnea, which normally infests shorthorns, was encountered in the spring before the fish supposedly moves offshore. Whether this movement can be attributed to a rise in water temperature or cryptic behavioral pattern of the host is unknown. Leeches are usually attached to the paired fins, especially the pectorals. Only infrequently are they found on the opercular chamber and ventrally on the body. They do not occur dorsally on the head, as does *M. scorpii*.

The number of *M. brunnea* on shorthorns increased with the advent of spring. Of 7 shorthorns examined in January (water temperature [WT] −0.5 C), each of 5 fish harbored 1 leech (20–35 mm), while the other 2 had 7 and 28, respectively. The latter ranged in length from 9 to 35 mm. More leeches were taken on shorthorns from April through June than earlier in the year. In one instance, 37 specimens were col-

TABLE 1. Effect of water temperature (WT) on cocoon deposition of *Malmiana brunnea* attached (A) to *Myoxocephalus octodecemspinosus* and unattached (U), during 75 days, in the laboratory.

Group	Temp (C)	No. of leeches	Cocoons deposited	Avg cocoon/ leech
1	−1.5	20 (A)	33	0.9
2	−1.5	40 (U)	271	6.8
3	5.0	20 (A)	153	7.7
4	5.0	20 (U)	267	13.4

lected from a single fish. Moreover, the incidence of infestation was high in spring, decreasing slightly thereafter in summer (Table 2).

About 100 leeches were removed from shorthorns and not permitted to feed for 17 days, in an attempt to induce hunger, after which various fish were introduced and left for 1–3 days to determine whether or not leeches would attach. The species tested were: Newfoundland (Laval's) eelpout, *Lycodes lavalaei*; Vahl's eelpout, *L. vahlii*; Atlantic wolffish, *Anarhichas lupus*; and moustache sculpin, *Triglops murrayi* (mailed sculpin, according to Leim and Scott 1966), but no leeches attached even temporarily. However, exposure to shorthorns and longhorns resulted in permanent attachment until death ensued following cocoon deposition.

Life history — Young (4–7 mm) *M. brunnea* were observed at all times of the year in a population infesting 12 shorthorns in the laboratory (WT 2–4 C). This population came from stock collected in April 1969 and had built up over the years (1969–74). Richardson's (1970) types of *M. nuda* and Mace and Davis' (1972) material were derived from this stock population.

Cocoon deposition is also affected by water temperature. Low temperature (−1.5 C) not only slowed down the rate of cocoon deposition but also affected the number of cocoons produced, as shown in Table 1. Also fewer cocoons were deposited by leeches attached to their hosts than by unattached animals during the 75 days.

Leeches produced an overall average of 8.2 (4.8–11.6) cocoons per individual. Cocoons are deposited on the sides of laboratory containers and are remarkably similar to those of *M. scorpii*, but they are smaller and contain fewer eggs. Cocoons measure 1.6 (1.3–1.8) × 1.4 (1.2–1.6) mm. *Malmiana brunnea* produces up to 5 (average 3.1 [1.7–4.5]) young in each cocoon. Investigators report only 1 young per cocoon for other species of Piscicolidae: these include Selensky (1915: 234), who reported on *Platybdella fabricii* (Malm [= his *Crangonobdella murmanica* Selensky 1923]; Moore and Meyer (1951: 22), on *Notostomum cyclostoma*[2] Johansson [= their *Notostomobdella cyclostoma*]; Becker and Katz (1965: 1189), on *Piscicola salmostica*[3] Meyer; Llewellyn (1965: 521), on *Hemibdella soleae* van Beneden and Hesse; Gibson and Tong (1969: 436), on *Oceanobdella blennii* (Knight-Jones); and Sawyer and Hammond (1973; 381), on *Calliobdella vivida* (Verrill) [= their *Calliobdella carolinensis* Sawyer and Chamberlain]. Development and hatching is temperature-dependent. Cocoons deposited by leeches removed from their hosts in mid-March (WT −1.5 C) hatched 131 days later. In contrast, cocoons produced in April (WT 1 C) required 96 days to complete development and emergence of young, while cocoons deposited in June (WT 8 C) and August (WT 13 C) produced young in 71 and 42 days, respectively.

[2]An explanation of the binomen is warranted. On the assumption that the name *Notostomum* Levinsen, 1882 was preoccupied by *Notostomus* Milne-Edwards, 1881 (Ann. Sci. Natur. Zool. Ser. 6, 11(4): 7) for a genus of Crustacea and hence, as a junior homonym, was unavailable, Moore and Meyer (1951) proposed *Notostomobdella* nom. nov. to replace *Notostomum*. But the suppression of *Notostomum* as a junior homonym contravenes Article 56(a) of the International Code of Zoological Nomenclature, 1964. *Notostomum* is therefore the valid genus-group name. Vasileyev (1939) synonymized *Notostomum cyclostomum* Johansson, 1899 and *Carcinobdella kanibir* Oka, 1910, but used the name *Carcinobdella* Oka, 1910 because he believed that the annulation of complete segments of *cyclostoma* more closely resembled those of *Carcinobdella* than that found in the type species of *Notostomum*, *N. laeve* Levinsen, 1882. Epshtein (1967) has shown that the annulation of complete segments of the 3 named species is identical; thus the proper binomens are *Notostomum cyclostomum* [= *Carcinobdella kanibir*] and *N. laeve*.

[3]Opinion is divided whether *Piscicola salmostica* Meyer, 1946 is the proper binomen, so we prefer to use the currently accepted name without any commitment as to the status of *Cystobranchus salmositicus* (Meyer) Epshtein 1969 (Problems in Parasitology, p. 286–287. *In* A. P. Markevich [ed.] Proc. Sci. 6th Conf. Parasitol. UKSSR, Kiev. Vol. 2.

Limited laboratory data suggest that *M. brunnea* has the potential of 2 generations each year. Cocoons deposited in the laboratory in April, 1973, hatched in July. The young (F_1) matured 46 days later and subsequently deposited cocoons. The latter underwent an incubation period of 54 days, the young (F_2) emerged in November, and matured in the spring of 1974. This pattern could be offset by water temperature. For example, in 1974, lower water temperatures occurred. Cocoons deposited in April–May did not hatch until late July and the young (F_1) that emerged did not produce cocoons until spring (1975) of the following year. The fact that young occur at all times of the year in our laboratory population coupled with observations of emerging young in November 1973 supports the hypothesis that *M. brunnea* is capable of producing 2 generations of young each year. We believe, however, that this might not occur in the field. Records from Logy Bay at a depth of 16–20 m, where divers normally encounter sculpins, indicate that water temperatures are consistently lower (1–2 C) than sea water pumped into the laboratory. The lower temperatures would be sufficient to slow down egg development and growth of the emerged young to the extent that only one generation could be accomplished each year.

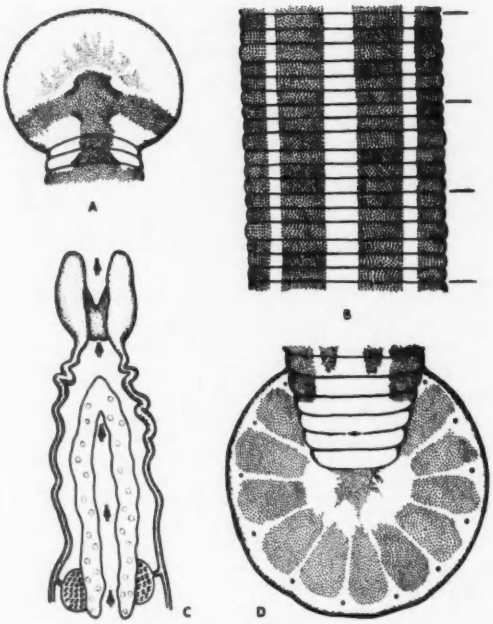

FIG. 2. *Malmiana scorpii*. A, Anterior sucker and adjacent trachelosomal rings; B, Three segments in region of testes; C, Reproductive system; D, Posterior sucker and adjacent urosomal rings. All dorsal views.

Malmiana scorpii (Malm, 1863)

Platybdella scorpii (partim) Malm, 1863: 253; *Ottonia scorpii* (partim): Malm 1874: 397; *Piscicola scorpii*: Levinsen 1883: 254; *Abranchus scorpii*: Johansson 1899: 680; *Ottonia scorpii*: Wessenberg-Lund 1926: 99; *Malmiana scorpii*: Strand 1942: 398 [by implication]; *Ottoniobdella scorpii*: Moore and Meyer 1951: 28; *Malmiana scorpii*: Epshtein 1962: 649; *Heptacyclus scorpii*: Epshtein 1967: 680.

ANATOMY

Body rounded, not flattened, and equally wide throughout; trachelosome not, or only slightly, narrower than urosome. Anterior sucker well developed and spread out, smaller than posterior sucker, which is wider than urosome. Anterior sucker faces anteroventrally, dilated, cupuliform to slightly discoidal, with thin marginal membrane. Urosome attenuated where posterior sucker joins, thus forming well-defined sucker peduncle. Up to 35 mm in length; widths of trachelosome and urosome, 1.4 and 1.5 mm, respectively; transverse diameter of expanded oral and anal suckers, 1.4 and 2.1 mm, respectively. Ratios for the body widths and sucker diameters true for only adults. In young, suckers are relatively more developed and their diameters considerably exceed greatest body width.

Three pairs of eyes, all generally crescent-shaped. Anterior pair, situated about equatorially on sucker, have crescents directed anterolaterally; second pair, slightly larger and closer together, face posterolaterally. Somewhat smaller crescents of third pair, on second ring, face forward and outward like first pair (Fig. 2). Eyes often varied; sometimes one or other of the pairs altered in shape or fragmented. Mouth or proboscis pore, surrounded by slightly raised area, located slightly postequatorially.

Posterior sucker well developed; circular, deeply cupped, eccentrically attached, and directed posteroventrally. Both suckers show characteristic color markings. Postequatorially on anterior sucker prominent dark brown transverse band present, which includes first 2 pairs of eyes; anteriorly often with narrower, indistinct band. Clear nuchal region, as in *M. brunnea*, interrupted medially by longitudinal band of pigment, connecting body pigmentation with broad band on sucker. Posterior sucker with brown center, like the longitudinal banding, the margin being

whitish except for 14 brown rays which diverge toward outer edge. Dorsally near margin there is a circle of 10–14 ocelli (usually 14), which alternate with the brown diverging bars.

Body with prominent brown longitudinal stripes, or with brown spots arranged in longitudinal or transverse rows (Fig. 3C). Transverse banding much more noticeable in young. In adults basic color pattern consists of 5 whitish lines alternating with as many more or less uniform brown areas, which usually run almost the entire length of body. Whitish lines consist of middorsal stripe, from sucker to sucker, which usually widens slightly posteriorly, and much narrower pair of continuous or interrupted light lines situated paramarginally. These alternate with paired dark brown paramedian stripes, which may disappear before reaching posterior sucker, and a pair of marginals, which extend onto ventral surface. Ventral surface light brown, bordered on each side by narrow white stripes, which contact with the brown marginals referred to above. At both ends, somewhat wider posteriorly, a light colored band separating brownish area from suckers. This basic color pattern is somewhat variable; consequently variations can be expected when the description is based on limited or long preserved material, e.g., Levinsen (1883: 254), and Moore and Meyer (1951: 34).

From clitellar region to posterior sucker (about XII through XXIV), as pointed out by Moore and Meyer (1951: 38), a series of paired segmentally arranged ocelli present on annulus a2 (as many as 12 pairs of ocelli have been observed, but the number is usually fewer, and one of the pair is often missing. These segmental ocelli as well as the circle of similar ocelli on the posterior sucker, at least in *Platybdella fabricii*, consist of a sensory cell surrounded by pigment cells, according to Selensky 1915: 78).

Occurrence

Sweden, Malm (1874: 398); Greenland, Malm (1863: 256); Spitzbergen, Johansson (1899: 681); Faroes, Bruun (1928: 3); Iceland, Bruun (1938: 3); Banks off Newfoundland, Wrangel Isl., Epshtein (1961: 1123); Northwest Territories, Moore (1921: 3); Bering Sea, Moore (1898: 555); Kamtchatka, Commodore Isl., Vasileyev (1939: 57).

Remarks

This species resembles *M. brunnea*, from which it differs externally principally in the prominent brown longitudinal striping of the body, and internally in the structure of the male reproductive system.

Biology

Host–parasite relationship — Malmiana scorpii, which normally infested longhorns and only occasionally shorthorns, were also encountered in the spring as the fish supposedly moved inshore where the water temperature is higher (1–3 C). Leeches were usually attached dorsally on the head, particularly from about the eyes forward. They rarely occurred on the fins and in the opercular chamber. None was observed on the ventral surface, between the gill filaments, or in the buccal cavity.

As the water temperature rose, fewer leeches were found on both species of sculpins. Our observations are based mainly on longhorns, as fewer shorthorns are encountered after June. Sculpins taken in July and August are generally free of leeches (Table 2). Twenty-one *M. scorpii* (25–35 mm) were removed from 37 longhorns in late June 1972 (WT 7 C), compared to 87 leeches from 16 hosts taken in late April 1972 (WT 2 C). Probably as the water temperature rises, many leeches take their final blood meal and leave their hosts, preliminary to depositing cocoons.

Small leeches (4–12 mm) were encountered in September and are more numerous (12–17 mm) than those observed in spring. Larger leeches (9–17 mm) were observed in October through December. Unfortunately, there are no infestation data for January through March (WT −0.5 to 1 C).

To test host proclivity, about 300 leeches were removed from sculpins, held in an aquarium for 28 days or longer in an attempt to induce hunger, and various species of fish were added and left for 1–3 days. Fish were added individually and none was used more than once. The only fish to which the leeches attached were the 2 species of sculpins. Even when leeches were placed directly on any of the other species of fish, they did not attach. On several occasions, leeches did attach to inanimate objects smeared with mucus from sculpins. This suggests that the parasite–host bond is physiological rather than ecological. The 23 species of fish tested, with the number of times for each, include: 12 longhorns; 12 shorthorns; 12 winter flounder, *Pseudopleuronectes americanus*; 12 yellowtail flounder, *Limanda ferruginea*; 12 American plaice, *Hippoglossoides platessoides*; 12 Atlantic cod, *Gadus morhua*; 12 capelin, *Mallotus villosus*; 8 (Atlantic) sea raven, *Hemitripterus americanus*; 7

TABLE 2. Monthly infestation of the sculpins *Myoxocephalus scorpius* and *M. octodecemspinosus* with the leeches *Malmiana brunnea*, *M. scorpii*, and *Oceanobdella microstoma*, in the field.

	Myoxocephalus scorpius		*M. octodecemspinosus*	
	Malmiana brunnea	*Oceanobdella microstoma*	*M. scorpii*	*O. microstoma*
	No. infested/No. examined			
Jan.	7/7	—	—	—
Feb.	—	—	—	—
March	—	—	—	—
Apr.	21/21	9/21	17/17	10/17
May	32/32	7/32	40/44	21/44
June	15/15	2/15	67/72	16/72
July	5/7	0/7	13/77	1/77
Aug.	2/3	0/3	5/59	0/59
Sept.	—	—	16/37	0/37
Oct.	—	—	20/22	0/22
Nov.	—	1/6	9/9	—
Dec.	—	2/5	6/6	—

Lycodes lavalaei; 2 *L. vahlii*; 6 *Macrozoarces americanus*; 6 thorny skates, *Raja radiata*; 6 cunner, *Tautogolabrus adspersus*; 5 *Anarhichas lupus*; 2 spotted wolffish, *A. minor*; 4 lumpfish, *Cyclopterus lumpus*; 3 (Atlantic) seasnail, *Liparis atlanticus*; 3 American eel, *Anguilla rostrata*; 2 haddock, *Melanogrammus aeglefinus*; 2 spiny dogfish, *Squalus acanthias*; 2 northern hogfish, *Myxine glutinosa*; 2 threespine stickleback, *Gasterosteus aculeatus*; 1 *Triglops murrayi*.

Life history — Reproduction and development of *M. scorpii* were followed in the laboratory, at ambient and controlled water temperatures. Mating occurred while the leeches were still attached to their host. They usually made searching motions with their anterior ends, eventually intertwined and released spermatophores. They remained in coitus for less than 3 h; invariably spermatophore release occurred within an hour.

Cocoon deposition occurred sometime later, usually while the leeches were still on the host. The clitellar region was extended to the side of the aquarium or other suitable surface, the cocoon attached and the animal subsequently withdrew from it like removing a cigar from its band. Mating and cocoon deposition was similar to that in *Piscicola geometra* (Linn.) and *Calliobdella vivida*, as described by Brumpt (1901: 101), and Sawyer and Hammond (1973: 380) respectively. Cocoon deposition occurred from April through December, during which the WT varied from 1 through 13 C. This does not imply that leeches are not capable of producing cocoons from January through March (WT −1.5 to 0 C). In fact, cocoons were produced within 14 days when large gravid leeches (about 35 mm) were removed from their hosts and held in aquaria in running water (at −1.5 C). However, fewer cocoons were produced in contrast to leeches held at 5 C. Apparently attachment to the host fish in some way inhibited or impeded cocoon deposition at low temperatures (0–1.5 C). Unmated adults (14–22 mm) also produced spermatophores and deposited fertile cocoons within 14 days when removed from −1 C and held at 5 C.

An average of 8.9 (5.3–12.5) cocoons were produced by each leech. The cocoon case was pale initially but darkened somewhat with age. But it remained sufficiently transparent to observe through it the eggs and developing young. Viewed dorsally, the case and its marginal lip were oval in outline; in profile, it was rounded dorsally and flattened ventrally. On the convex surface, near the ends of the longitudinal axis, marking the closures in the deposition of the cocoon, there were darkly colored areas, which, however, differed in structure; the smaller was papilliform, while the larger, through which the young escape, resembled the operculum of a trematode egg.

Again, in contrast to other species of Piscicolidae, more than one embryo were found in each cocoon. Two markedly different sizes of cocoons were produced; one, 1.6 (1.4 − 1.8) × 1.3 (1.2 − 1.4) mm, contained on an average 2 (1–3) eggs, while the other, 2.2 (2.0 − 2.4) × 1.8 (1.5 − 2.1) mm produced an average of 5 (4–8) young. While the smaller leeches (14–22 mm) apparently produced only small cocoons, and the

TABLE 3. Effect of water temperature (WT) on cocoon deposition of *Malmiana scorpii*, in the laboratory.

WT (C)	Young emerged	Cocoons deposited	Days required
8–13	13 VII 1973 (F_1)[a]	20 VIII 1973	48
12–13	8 VIII 1973 (F_1)	14 IX 1973	35
8–12.5	13 VIII 1973 (F_1)	20 IX 1973	38
8–13	8 IX 1973 (F_2)	26 X 1973	48
−1.5–8	3 X 1973 (F_2)	27 IV 1974	206

[a]Filial generation.

TABLE 4. Effect of water temperature (WT) on cocoon hatching of *Malmiana scorpii*, in the laboratory.

WT (C)	Cocoons deposited	Young emerged	Days required
1–8	30 IV 1973	13 VII 1973 (F_1)[a]	74
12–13	30 VIII 1973	4 X 1973 (F_2)	35
9–13	12 IX 1973	20 X 1973 (F_2)	38
7–13	20 IX 1973	6 XI 1973 (F_2)	50
5	20 II 1974	7 V 1974 (F_3)	75
0–5	30 XI 1973	13 IV 1974 (F_3)	134
−1.5–8	13 III 1974	23 VII 1974 (F_3)	132
−1.0–8	20 IV 1974	21 VII 1974 (F_3)	92

[a]Filial generation.

larger leeches (about 35 mm) produce primarily large cocoons, there was no apparent correlation between the size of the leech and the number of cocoons produced.

The occurrence of 2 markedly different sizes of leeches, each producing not only a cocoon of a distinct dimension but also differing in the number of eggs per cocoon, appeared to be related to the number of leeches attached to each host in the laboratory (the smaller type [14–22 mm] has not so far been observed on sculpins naturally infested with *M. scorpii* in spring). When large numbers (between 100 and 400) of leeches are present on longhorns, their sizes at the time of maturity varied from 14 to 22 mm. In contrast, whenever small numbers (about 50 or fewer) occurred on the fish, most attained their maximum length (about 35 mm). Since large leeches are normally the type collected in the field, and since the smaller type has occurred on fish on at least 6 different occasions in the laboratory, crowding probably results in smaller leeches being produced.

While 25–50 ml glass jars and aquaria were utilized as a site for cocoon deposition, if stones and bivalve shells are provided, many more cocoons are deposited on these objects. This observation prompted us to examine stones and bivalve shells present in areas frequented by sculpins. Several cocoons were observed on these objects, and the young which emerged were those of *M. scorpii*. Leeches deposited cocoons from 35 days onwards at peak temperatures of 13 C (Table 3).

After depositing cocoons, leeches gradually lose their color especially in the clitellar region. Eventually, they detach from their host and fall to the bottom of the aquarium, where they remain until death ensues. This varies from 4 to 14 days, being more rapid at higher temperatures. Leeches "die" from the posterior end forward, as do the plerocercoids of tapeworms.

Young leeches (3–6 mm) emerged from cocoons after a period of incubation that was temperature dependent. It varied from 35 days at peak ambient temperatures (13 C) to 134 days at 0–5 C (Table 4). Growth of the young was slow during the first 3 wk after emergence. They did not feed and therefore probably depended on the stored food materials present in the egg, as do other Piscicolidae. Growth was then rapid. At peak water temperatures (13 C) they grew at the rate of 0.8–2.3 mm each week, while at lower temperatures (0–5 C) growth was consistently less than 1 mm/wk.

Dissection of leeches at various intervals during

life history led us to believe that 3–5 blood meals are taken following emergence up to cocoon deposition. Again, time of digestion of the blood was temperature dependent being most rapid during early August to late September (13 C). Sizes attained by leeches grown under laboratory conditions were never as large as those taken in the field. On account of the large sizes of some leeches encountered in the field in September, possibly a few might survive for more than one breeding season, or more likely they represented mature offspring (F_1) of that year.

A reconstruction of the life history of *Malmiana scorpii* is proposed on the basis of 4 yr of extensive laboratory studies and limited field data. Leeches were first observed on longhorns and shorthorns between late March and early April of each year. Each adult leech (P_1 generation) deposited up to 13 cocoons on stones or bivalve shells from April through June. At the ambient temperature (1–8 C) young leeches (F_1) began to emerge about mid-July, the complete embryonic development being achieved in 74 days. Young leeches measured 4.5 (3–6) mm. They grew, and matured about 48 days after emergence. At this stage, they measured about 18 (15–21) mm. Water temperature at this time (late August) was at its highest (13 C). Leeches continued to grow and deposit cocoons, attaining a maximum size of about 28 (24–31) mm. From 50 days after emergence, they began to die and by 90 days all of 300 leeches were dead (WT 11 C).

Cocoons deposited towards the end of August (WT 13 C) hatched in about 35 days. The emerging young (F_2) fed and grew rapidly (0.4–1.8 mm/wk), with cocoon deposition beginning 44 days after emergence when about 12.5 (10–14) mm. Cocoon deposition ceased by mid-December (WT 3 C). Some of the leeches (about $\frac{1}{10}$ of 300) died. It was presumed that the latter represented leeches that had deposited their full complement of cocoons. Growth of surviving leeches at this time had slowed down considerably. They measured 21.8 (17–23) mm. Most attained a length of 29 (26–32) mm 134 days after emergence. Many commenced to deposit cocoons in April (WT 1 C) of the following year.

Leeches (F_2) which emerged in October (WT 12 C), measured 14.2 (13–15) mm in 80 days by mid-December. Despite the fact that viable sperm were present in many, there was no evidence of copulation or cocoon deposition until the following spring. Examination of sectioned material taken in February (WT −1 C) indicated that the ova were not fully developed. Apparently higher water temperatures (13 C) increased the rate of development of eggs, whereas extremely low temperatures slowed down development considerably. These leeches produced cocoons approximately 206 days after emergence.

Oceanobdella Caballero, 1956

Body rounded; body wall relatively unpigmented and transparent, weakly divided into trachelosome and urosome; no collar, tubercles, pulsatile vesicles, or other paired lateral structures; anterior sucker very small, posterior sucker well developed.

The shape of the oral sucker and the weak body musculature seem to be the most usable characters for separating *Oceanobdella* and *Malmiana*.

Oceanobdella microstoma (Johansson, 1896)

Abranchus microstomus Johansson, 1896; 34; *Oceanobdella microstoma*: Caballero, 1956: 282; *Oceanobdella microstomata*: Soós, 1965: 442.

Anatomy

Trachelosome narrower than urosome, which is more or less flattened. Anterior sucker, small, quite unnoticeable. When at rest, size and shape agree closely with illustrations of Johansson (1896: pl. VII, figs. 70, 71, 72; 1929: fig. 13) (only when the animal attaches to some object by the oral sucker does it become slightly distinct from trachelosome, and the otherwise somewhat swollen edge becomes extended to form a narrow disc).

Three pairs of eyes, situated as in *M. scorpii*, but not so crescent-shaped (Fig. 4). Darkened area of finely branched pigment cells, forming cross-like structure between first two pairs and third pair of eyes; similar pigmented areas sparingly scattered dorsally on anterior part of the body. Mouth or proboscis pore slightly anterior to first pair of eyes. Posterior sucker well developed; in preserved specimens, broader than widest part of urosome. Near periphery of sucker circle of about 10 ocelli present, although the number varies from 2 through 12. No diverging rays between ocelli, as in 2 above species. There is, however, a wedge-shaped patch of branched pigment on the sucker that normally includes the 3 most posterior ocelli. From clitellum to posterior sucker (about XII through XXIV), each segment may have up to 2 pairs of ocelli situated on a2, but usually only one pair is seen. While the number of pairs varies, 14 being the maximum, 12 is the usual number.

Because of weak development of body wall

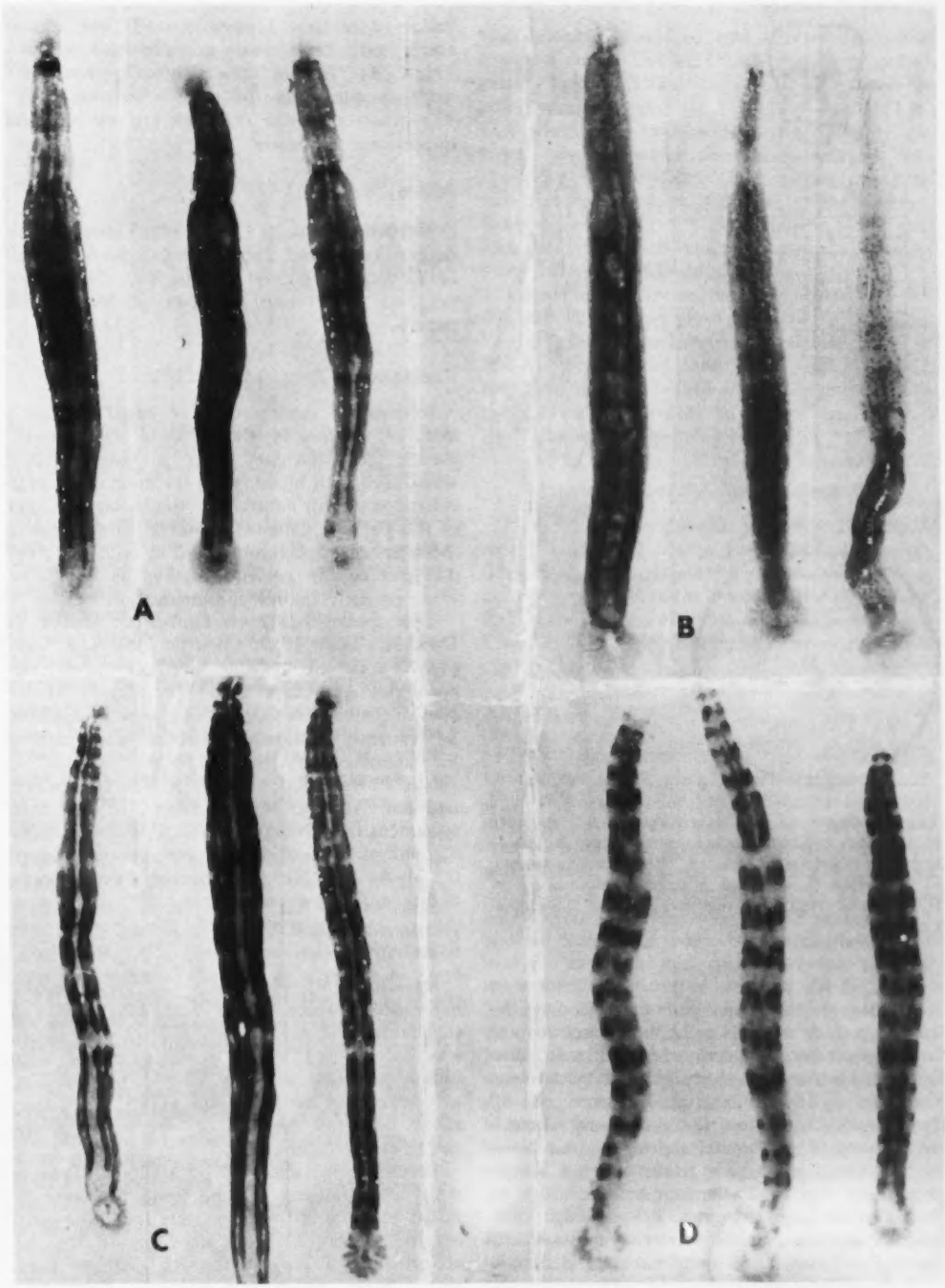

FIG. 3. Photographs of leeches anesthetized in 15% ethanol: A, *Malmiana brunnea* (the white spots are small air bubbles); B, *Oceanobdella microstoma*; C, *M. scorpii*; D, *O. sexoculata*. All dorsal views.

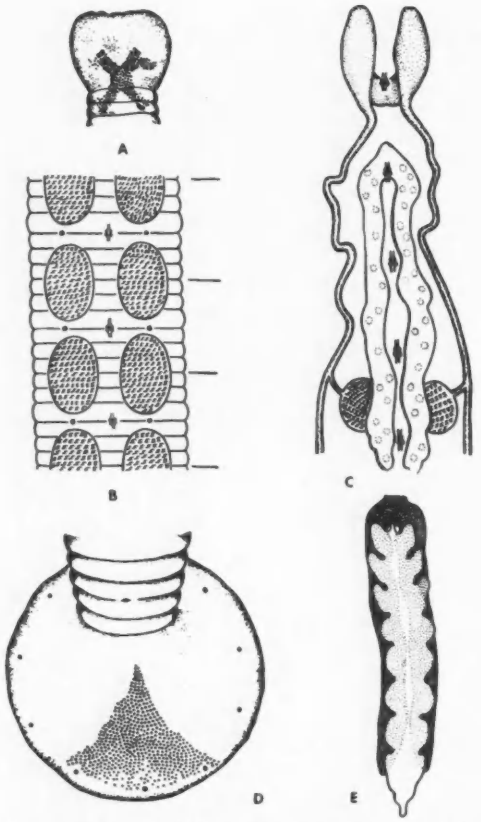

FIG. 4. *Oceanobdella microstoma*. A, Anterior sucker and adjacent trachelosomal rings; B, Three segments in region of testes; C, Reproductive system; D, Posterior sucker and adjacent urosomal rings; E, Posterior region of digestive system. All dorsal views.

muscles, in life urosome in passive state more or less flattened, sometimes prominently so, therefore its greatest width is 2–2.5 mm. Trachelosome much narrower, decidedly less flattened than urosome; increases slightly in width posteriorly. Clitellum usually distinct, usually sharply set off from preclitellar region. Urosome usually broadest forward of the middle, and tapers from there in both directions, which makes posterior sucker prominent. Up to 25 mm in length; width of trachelosome and urosome, 0.7 and 1.0 mm, respectively; transverse diameter of oral and expanded anal sucker, 0.7 and 1.8 mm, respectively.

Body almost entirely unpigmented, rather translucent-yellowish because of numerous salivary and cocoon glands which show through. Small yellow dots thus formed spread over almost entire body, much more dorsally than ventrally (Fig. 3B). In life cuticle often shows small ridge- or papilla-like folds, as Johansson (1896: 47) observed. These markings are not apparent in preserved specimens.

OCCURRENCE

Sweden, Johansson (1896: 36); Finland, Spitzbergen, Greenland, Johansson (1899: 682); Iceland, Wesenberg-Lund (1926: 98), Newfoundland and south into the Gulf of Maine (this paper).

REMARKS

Johansson's description was based on living material; because in life the body wall is transparent the alimentary tract is visible which, when filled with blood, gives the animal a beautiful red color. In addition to the blood-red color of the gut, the flattened urosome, in contrast to the rounded trachelosome, and in relation to the diameter of the posterior sucker, is seen convincingly only in live specimens.

This species has been known to one of us (M.C.M.) since 1939, when the late H. J. VanCleave collected it from shorthorns and longhorns, off Appledore Island (in Maine) of the Isles of Shoals near Portsmouth, New Hampshire. Subsequently additional material was received for identification from graduate students of Wilbur L. Bullock, University of New Hampshire, Durham. After examining many live and fixed specimens from Newfoundland, it is now possible to confirm the earlier tentative identification of the Maine–New Hampshire leeches from sculpins, as *Oceanobdella microstoma*.

BIOLOGY

Host–parasite relationship — Oceanobdella microstoma, which infests both longhorns and shorthorns, and occasionally *Lycodes reticulatus*, was encountered in the spring. Leeches were usually attached ventrally on the head region, as pointed out by Johansson (1896: 35). They rarely occurred dorsally on the head, in the mouth or opercular cavity.

Leeches were observed on sculpins taken in April and May but in June fewer fish were infested and by mid-July none were found parasitizing fish (Table 2). Nor were any of the fish collected from August through October parasitized. Small leeches were, however, observed on 1 fish captured in November, and 2 of 5 taken in December also harbored small forms.

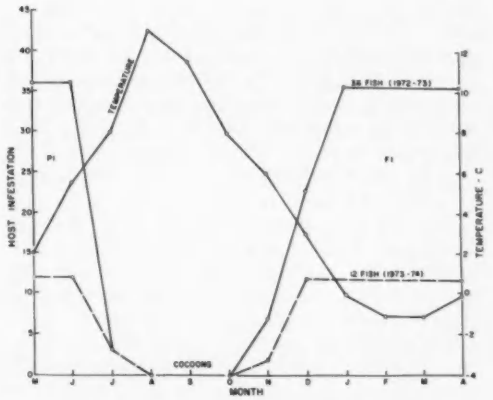

FIG. 5. Monthly infestation of *Myoxocephalus scorpius* with *O. microstoma*, each involving two generations in the laboratory (1972–73 and 1973–74).

Thirty *O. microstoma* which had been withheld from fish for 62 days, at about 5 C, were exposed to 10 species of fish for 1–3 days to determine whether or not they would attach. Leeches did not attach to 4 *Anarhichas lupus*; 4 *Gadus morhua*; 2 *Macrozoarces americanus*; 2 *Raja radiata*; 2 *Cyclopterus lumpus*; 6 *Hemitripterus americanus*. But they did attach and fed readily (ingested blood is easily detected through the transparent body wall) on 2 longhorns, 2 shorthorns, 2 *Lycodes reticulatus*, and 2 *L. vahlii*. These results suggested that *O. microstoma* may have a wider range of host tolerance than *Malmiana brunnea* and *M. scorpii*.

Life history — Cocoon deposition was water temperature related. In 2 successive yr, involving 48 shorthorns, in July (8 C) and August (maximum 13 C) leeches left their hosts and deposited cocoons (Fig. 5). Since they die shortly after depositing cocoons, the fish were relatively free of leeches until November and December, when they were again infested with the young leeches.

Oceanobdella microstoma produced an average of 17.6 (6.8–28.4) cocoons per individual. Ten leeches which had survived up to 36 days at 1–2 C in spring from the onset of cocoon deposition, produced an average of 1 cocoon per day for 28 days. These leeches had commenced depositing cocoons from 6 to 11 days inclusive, after removal from their hosts. When held in 25 ml glass jars, they deposited cocoons in clutches of about 5 or in a straight line. In aquaria, the sides rather than the bottom sites were preferred, but stones and empty bivalve shells were chosen if offered.

In correlation with the smaller diameter of the trachelosome, compared with that of *Malmiana brunnea* and *M. scorpii*, *O. microstoma* produced smaller cocoons. They were yellowish-brown in color, and measured 1.3 (1.0–1.4) × 1.1 (1.0–1.2) mm. Each cocoon had two "plugs"; the larger, through which the young escaped, was about 219 μm in diam. One embryo was contained in each cocoon. Cocoons at the ambient temperature (0–11 C) deposited in May and June did not hatch until November, requiring about 161 (137–189) days.

Young leeches measured 2.3 (2.1–2.4) × 0.3 (0.2–0.3) mm. They grew more rapidly at higher temperatures. At ambient temperatures (−1.5 to 3 C), they matured towards the end of April, requiring 166 (152–181) days. The cycle of *O. microstoma* is therefore an annual one as only 1 generation was produced each year.

Oceanobdella sexoculata (Malm, 1863)

Platybdella sexoculata Malm, 1863: 226; *Piscicola sexoculata*: Levinsen 1883: 254; *Abranchus sexoculatus*: Johansson 1896: 36; *Platybdella buccalis* Nigrelli 1946: 215; *Oceanobdella sexoculata*: Caballero 1956: 282; *Oceanobdella sexoculata*: Epshtein 1962: 649; *Platybdella buccalis*: Sawyer et al. 1975: 654.

ANATOMY

Trachelosome narrower than flattened urosome. Oral sucker small, when at rest nearly retracted. Anal sucker well developed, broader than urosome at its broadest place. Body heavily pigmented with small black dots arranged in transverse bands. Three pairs of eyes, shaped and placed as in *O. microstoma*. Up to 23 mm in length; width of trachelosome and urosome, 1.1 and 1.6 mm, respectively; transverse diameter of oral and expanded anal sucker, 0.7 and 2.0 mm, respectively.

Basic color of body yellowish-white, from salivary and cocoon gland cells which show through. Entire dorsal surface covered with broad segmentally arranged transverse bands, broken middorsally, consisting of small dots (Fig. 3D). On urosome posteriorly, large black spots along lateral margins, formed by flecks more closely spaced. Lateral markings and transverse bands are situated intersegmentally.

On trachelosome, separated by a clear space from bar on sucker, 5[4] dark transverse bands present. First 4, of equal width, less than half as wide as the fifth, which includes clitellum.

[4]Malm (1863: 227) says there are 6 bands, but this obviously includes the band on the oral sucker.

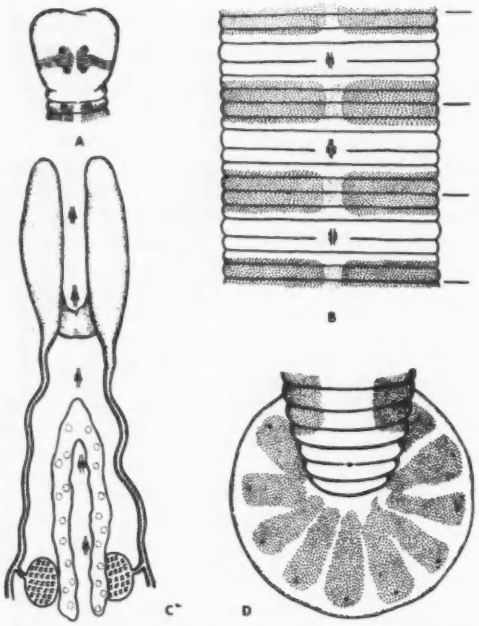

FIG. 6. *Oceanobdella sexoculata*. A, Anterior sucker with adjacent trachelosomal rings; B, Three segments in region of testes; C, Reproductive system; D, Posterior sucker and adjacent urosomal rings. All dorsal views.

Eleven bands on urosome, first 5 of which are equally wide, separated by white bands of same width as dark bands. These followed by 6 dark colored, somewhat broken bands, each of which is separated by a slightly wider band, with prominent dark spots along lateral margins.

First and second pairs of eyes separated by dark transverse band, which is weakly divided middorsally (Fig. 6). Dark spot with weakly diverging bars dorsally on anal sucker. Circle of ocelli situated at outer ends of diverging bars, not between bars as in *Malmiana brunnea* and *M. scorpii*.

OCCURRENCE

Sweden, Malm (1863: 228); Johansson (1896: 39; 1899: 682); Bering Sea, Moore (1898: 555); Western Atlantic (vicinity of New England), Nigrelli (1946: 215); Massachusetts, Sawyer et al. (1975: 655); Newfoundland and Gulf of Maine (this paper).

REMARKS

In none of the *O. sexoculata* examined was there a circle of ocelli on the oral sucker, as stated by Johansson (1896: 36). Reference to these ocelli by Johansson is clearly a *lapsus calami*; for there is nothing in Malm's detailed description or in his illustration (pl. 4, fig. 16a), based on live material, to indicate the presence of a circle of ocelli on the oral sucker. This fictitious character repeated by Johansson (1899: 682; 1929: 140) and incorporated in the key by Herter (1935: 53) has been corrected by Knight-Jones (1940: 540; 1962: 177).

The apparent rareness of the leech may be because its hosts are much more difficult to collect than are sculpins, and the fact that the leeches escape notice unless a special search is made for them in the mouth of the fish.

Superficially *O. sexoculata* looks like *O. blenni* (Knight-Jones, 1940), which it resembles in many particulars except for choice of host, location, and size.

The description of *Platybdella buccalis* Nigrelli, 1946 is so undiagnostic, being limited to general body shape and eyes, that it is hardly possible to identify the form the author had in mind. Unfortunately, the eyes which Nigrelli chose as diagnostic between *Oceanobdella sexoculata* [= his *Abranchus sexoculatus*] and some other related species are ephemeral. For, as shown for *Malmiana brunnea* (Fig. 1), the pigmentation, including the melanin series of the eyes and ocelli, fades and may even disappear completely with long preservation of specimens. In a paratype[5] of *P. buccalis*, in the USNM (Helm. Coll. 52716), the 2 pairs of eyes have faded and are no longer discernible.

Therefore, Nigrelli's failure to detect the third pair of eyes, the circle of ocelli on the anal sucker, and striking color markings, so characteristic of *O. sexoculata*, is relatively unimportant for 2 reasons. First, there is no evidence that he employed cleared specimens, which is common practice in detecting eyes and similar markings; and second, because long preservation had likely blanched these diagnostic markings.

The fact that *P. buccalis* occurred in the mouth of *Macrozoarces americanus*, the identical location of the same host species as our *O. sexoculata*, lends further support to the belief that *P. buccalis* is conspecific with *O. sexoculata*.

BIOLOGY

Host–parasite relationship — Our material was obtained primarily from the mouth and infrequently from the trunk and fins of oceanpouts. Seventy six *O. sexoculata* (15–23 mm) were obtained from 14 oceanpouts (13/14 infected)

[5]Sawyer et al. (1975: 655), on the assumption that the types were lost, designated neotype and neoparatypes.

collected from April through June. Two of five oceanpouts, taken in July, were infected with 8 mature leeches but none of 6 fish, collected through August and September harbored leeches. One (6 mm) was removed from an oceanpout collected in October, whereas 2 (10 and 15 mm) were obtained from 2 fish caught in November. A single fish, collected in February, was infested with one leech (17 mm) while another in March harbored 237 leeches measuring 19.0 (12–23) mm. Twenty-six of the latter (19–23 mm) deposited cocoons when removed to individual aquaria. Two *O. sexoculata* were also collected by E. M. Burreson from the mouth of an oceanpout, taken 2 mi south of Hampton Harbor, New Hampshire, USA in July 1975.

Twenty-seven newly emerged *O. sexoculata* were exposed sequentially at 14 C to a longhorn, shorthorn, Atlantic cod, cunner, and oceanpout. Leeches attached only to the oceanpout. They migrated subsequently from the trunk to the angles of the buccal cavity where engorgement occurred. Eleven unengorged leeches (14–21 mm) were also exposed in sequence to a winter flounder, longhorn, Atlantic cod, and oceanpout but attached only to the latter. When *Lycodes lavalaei*, a familial relative of both *Zoarces viviparus* and *M. americanus*, were added to a tank containing 14 hungry *O. sexoculata*, the leeches showed a "host awareness," characterized by a searching response and attachment to the fish within 30 min. An additional 16 unengorged leeches fed readily when placed on an *L. lavalei*. These results suggest a degree of specificity at the family level.

Life history — Twenty-six leeches held in separate aquaria at 0–4 C deposited 16.6 (8.8–23.8) cocoons over 28 days. Thus fecundity of *O. sexoculata* is apparently similar to that of *O. microstoma*. The cocoons, pale brown in color, measured 1.5 × 1.2 (1.7 − 1.2) × (1.4 − 1.2) mm and were deposited on the sides of the aquaria.

One embryo was contained in each cocoon. The latter, when deposited in May–June hatched at the ambient temperature (6–16 C) in August, that is within 60 days. The young measured 2.0 (1.8–2.2) × 0.25 (0.2–0.3) mm. After 45 days at 11–16 C, 5 specimens measured 9 (7–11) mm, 18 (15–21) mm after 102 days at the ambient of 5–11 C, and 22 (21–23) mm after 200 days at 0–5 C. The latter animals although mature remained within the buccal cavity of their host, but were capable of depositing cocoons at 157 days following removal to an aquarium. Since adult leeches were removed from a fish collected from the field in March, probably those noted in February (200 days) remain attached to their hosts until spring before detaching and depositing cocoons. The life cycle of *O. sexoculata* appears therefore to be annual.

Discussion

Malmiana scorpii appeared to have envolved a unique relationship with its fish host. Unlike most Piscicolidae, which detach from their hosts prior to copulation and cocoon deposition, *M. scorpii* remained permanently attached to longhorns. The latter observation may perhaps be a significant factor in cocoon distribution over the fish's habitat and would ensure that some of the emerging young locate a suitable host. Moreover, the lethargic habits of the fish renders it prone to infestation by these leeches. These observations also apply to *M. brunnea* but less information is available. Both *O. microstoma* and *O. sexoculata* leave their hosts prior to mating and cocoon deposition and resembled most piscicolid leeches in this respect. Also, both species produced 1 young per cocoon in contrast to *M. scorpii* and *M. brunnea*, which produced more than 1 young in each cocoon.

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Theoretical and Experimental Analysis of the ^{14}C Technique and Its Use in Studies of Primary Production

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HOBSON, L. A., W. J. MORRIS, AND K. T. PIRQUET. 1976. Theoretical and experimental analysis of the ^{14}C technique and its use in studies of primary production. J. Fish. Res. Board Can. 33: 1715–1721.

Theoretical and experimental field studies of ^{14}C uptake by marine phytoplankton were carried out to determine environmental conditions required for the technique to measure net photosynthesis. Results of theoretical studies indicate that rapidly metabolizing populations (rate constants for gross photosynthesis and respiration of 0.1 h^{-1} and 0.007 h^{-1}, respectively) may saturate with ^{14}C after about 30 h of continuous irradiation. Results of field studies indicate that a minimum of 24 h are required for net photosynthesis to be measured when daily irradiations exceed 20 cal cm^{-2} and nutrient limitation of photosynthesis does not occur. Additional measurements that may be made to aid in interpreting results obtained by the ^{14}C technique are briefly discussed.

HOBSON, L. A., W. J. MORRIS, AND K. T. PIRQUET. 1976. Theoretical and experimental analysis of the ^{14}C technique and its use in studies of primary productivity. J. Fish. Res. Board Can. 33: 1715–1721.

Nous avons fait des études théoriques et expérimentales sur le terrain de l'absorption du ^{14}C par le phytoplancton marin en vue de déterminer les conditions du milieu nécessaires à la mesure de la photosynthèse nette. Les résultats des études théoriques démontrent que les populations à métabolisme rapide (constantes de taux de photosynthèse brute et de respiration de 0.1 h^{-1} et de 0.007 h^{-1} respectivement) peuvent être saturées de ^{14}C après 30 h environ d'irradiation continue. Les résultats des études sur le terrain démontrent qu'il faut un minimum de 24 h pour mesurer la photosynthèse nette quand les irradiations quotidiennes dépassent 20 cal cm^{-2} et qu'il n'y a pas limitation de photosynthèse. Nous examinons brièvement les déterminations supplémentaires à faire pour aider à interpréter les résultats obtenus par la méthode du ^{14}C.

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THE ^{14}C technique for measuring primary productivity was developed and first used by Steemann-Nielsen (1952). Often it is used to study the effect of depth (i.e. irradiance) on phytoplankton productivity (e.g. Ryther 1963) assuming that the technique measures identical productivities when cells are exposed to varying irradiances. The purpose of the present study was to examine this assumption. This examination initially was carried out by a theoretical study of time courses of ^{14}C uptake and intracellular ^{14}C:^{12}C ratios by cells having varying photosynthetic and respiratory rates. These two parameters were chosen because ^{14}C uptake can be easily measured and may be related to intracellular ^{14}C:^{12}C ratios which determine what the ^{14}C technique measures. For example, when ratios are infinitely small the technique measures gross productivity, and when ratios are at equilibrium with extracellular ratios the technique measures net productivity. Results of this study did not support the assumption of comparability of productivities, and these results were indirectly verified with populations of microplankton in Saanich Inlet, a fjord on Vancouver Island, B.C. Results of these studies are summarized in this paper.

The Model

Ratios of total carbon, ^{12}C, and ^{14}C accumulated by cells can be modeled by:

$$\frac{dC(t)}{dt} = P \cdot C(t) - R \cdot C(t) \qquad (1)$$

$$\frac{dC_{12}(t)}{dt} = \frac{P \cdot C(t)}{1 + K} - R \cdot C_{12}(t) \qquad (2)$$

$$\frac{dC_{14}(t)}{dt} = \frac{K \cdot P \cdot C(t)}{1 + K} - R \cdot C_{14}(t) \qquad (3)$$

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where P and R are rate constants for gross photosynthesis and respiration (t^{-1}), K is the ratio of ^{14}C:^{12}C in the extracellular environment, and $C(t)$, $C_{12}(t)$, and $C_{14}(t)$ are amounts of total carbon, ^{12}C and ^{14}C accumulated by cells at time t. Solutions for $C(t)$, $C_{12}(t)$, and $C_{14}(t)$ are:

$$C(t) = C_0 e^{(P-R)t} \tag{4}$$

$$C_{12}(t) = \frac{C_0}{1+K}\left[e^{(P-R)t} + K \cdot e^{-R \cdot t}\right] \tag{5}$$

$$C_{14}(t) = \frac{K \cdot C_0}{1+K}\left[e^{(P-R)t} - e^{-R \cdot t}\right] \tag{6}$$

where C_0 is total carbon in cells at zero time. Dividing equation (6) by (5) gives:

$$\frac{C_{14}(t)}{C_{12}(t)} = \frac{K\left[e^{(P-R)t} - e^{-R \cdot t}\right]}{e^{(P-R)t} + K \cdot e^{-R \cdot t}} \tag{7}$$

which gives intracellular ratios of ^{14}C:^{12}C at any time, and these approach K when t approaches infinity. Assumptions that made these derivations possible are: 1) no time lag occurs between production of labeled substrated by the phosphoglycerate cycle and transport and decarboxylation of these substrates by the tricarboxylic acid and pentose phosphate pathways (Raven 1972a), and glycolate metabolism (Raven, 1972b), and 2) newly synthesized labeled substrates are equally available with unlabeled substrates to decarboxylation. The former assumption is incorrect, but any time lag that occurs will be negligible compared to the duration of a productivity experiment. The latter assumption is probably accurate when cells are dividing rapidly, but is probably inaccurate if cells are existing at suboptimal conditions for cell division, for example at compensation irradiation. Photosynthetic and respiratory rates were normalized on total carbon at zero time because these rates do vary among species and among physiological states of a given species. As organic carbon accumulates, these rates are assumed to remain constant in the model and are normalized on instantaneous concentrations of total carbon. This is the simplest case, and photosynthetic and respiratory rates could change with time in systematic or unsystematic ways. For example, Daley and Brown (1973) showed that ratios of photosynthetic rates to cell carbon were constant and increased for the blue-green algae *Phormidium molle* and *Anacystis nidulans*, respectively, during the exponential phase of cell division. Also, Griffiths (1973) showed that ratios of photosynthetic rates to cell numbers and to chlorophyll *a* decreased for the diatom *Phaeodactylum tricornutum* during the exponential phase of cell division.

Computations of time courses of ^{14}C accumulation and of ratios of ^{14}C:^{12}C in organic matter were made with equations (6) and (7) (Fig. 1 and 2). Boundary conditions included $K = 6.7 \times 10^{-4}$ based on 75 μCi/liter of $^{14}CO_2$ in sea water having 25 mg/liter of $^{12}CO_2$-C. The various values of C_0, P, and R were selected from data obtained from studies carried out with phytoplankton populations in the local marine environment. Results of these computations predict that

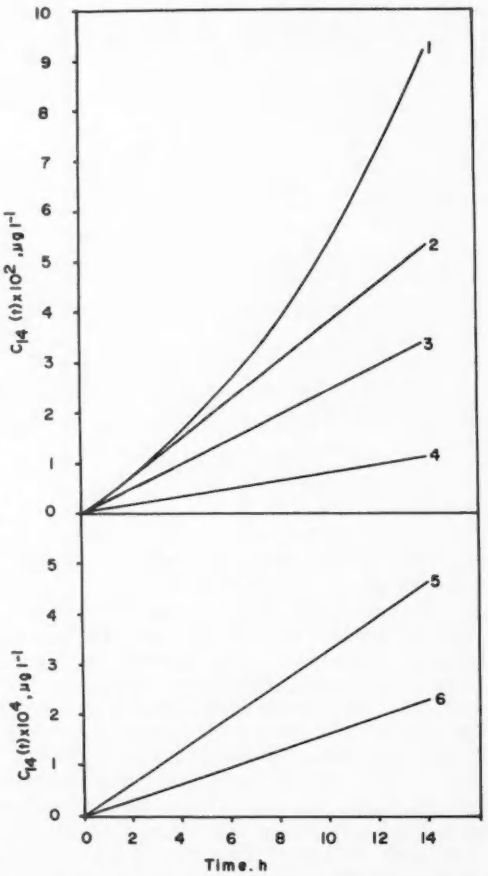

FIG. 1. Kinetics of ^{14}C uptake in hypothetical algal populations having: 1) C_0 = 50 μg liter^{-1}, P = 0.1 h^{-1}, R = 0.007 h^{-1}; 2) C_0 = 350 μg liter^{-1}, P = 0.015 h^{-1}, R = 0.001 h^{-1}; 3) C_0 = 350 μg liter^{-1}, P = 0.01 h^{-1}, R = 0.001 h^{-1}; 4) C_0 = 250 μg liter^{-1}, P = 0.005 h^{-1}, R = 0.001 h^{-1}; 5) C_0 = 50 μg liter^{-1}, P = 0.001 h^{-1}, R = 0.001 h^{-1}; and 6) C_0 = μg liter^{-1}, P = 0.0005 h^{-1}, R = 0.001 h^{-1}.

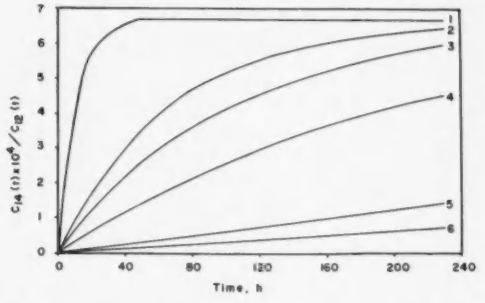

FIG. 2. Time changes in intracellular ratios of ^{14}C:^{12}C in hypothetical algal populations having boundary conditions given in Fig. 1.

rates of accumulation of ^{14}C by cells depend on net photosynthetic rates and that intracellular ratios of ^{14}C:^{12}C depend on gross photosynthetic rates. Carbon-14 activity was predicted to vary from about 1×10^6 dpm in cells with $P - R = 0.093\ h^{-1}$ and $R = 0.007\ h^{-1}$ to 2×10^3 dpm in cells with $P - R = -0.005\ h^{-1}$ and $R = 0.001\ h^{-1}$ after 14 h. With these two values of $P - R$ about 30 h and greater than 1000 h (in continuous light) would be required for intracellular ratios of ^{14}C:^{12}C to be within 95% of K. Thus, the model predicts that net photosynthetic rates frequently may not be measured in nature where environmental conditions depress gross photosynthetic rates. These conclusions were tested on populations of marine phytoplankton.

Field Observations

Materials and Methods

A station in Saanich Inlet was occupied periodically from February to October 1973 by the Department of Transport's motor launch *Vancouver* II. Seawater samples were collected at various depths by Niskin bottles, and these samples were used to determine phytoplankton carbon and productivity. Phytoplankton carbon was estimated by two indirect methods: 1) microscopic analysis and 2) chlorophyll *a* analysis. Microscopic analyses have been outlined by Hobson et al. (1973) and include: 1) preservation of phytoplankton by Lugol's solution, 2) concentration of preserved cells by sedimentation, 3) examination, counting, and measurement of cells with an inverted microscope, and 4) estimation of cell carbon by factors relating cell volume to cell carbon. Chlorophyll *a* concentrations were converted to carbon concentrations assuming a ratio of 25 between cell carbon and chlorophyll *a*. Pigment concentrations were determined by the spectrophotometric technique described by Richards with Thompson (1952) and by Creitz and Richards (1955) using the equations given by Parsons and Strickland (1963). Phytoplankton production was estimated by the ^{14}C technique (Steemann-Nielsen 1952) employing 265-ml light and dark bottles. Samples were taken from various depths and aliquots of these samples were siphoned into light and dark bottles, and these aliquots were incubated with 10 μCi of $H^{14}CO_3^-$ for 24 h while attached to a free-floating buoy at depths from which the samples were taken. All shipboard operations were carried out either in darkness or dim light. After removing bottles from the buoy, aliquots were filtered through Millipore AA filters (0.8-μ pore diam) by a vacuum of less than 5 mm Hg. Filters were rinsed with filtered sea water, placed over fumes of concentrated HCl for 15 min, and dried at 60 C for 20 min. Dried filters were placed in 10 ml of Econofluor (New England Nuclear) for counting. Filtrates without washings were acidified by 50 μl of concentrated HCl to give a final pH less than 2, bubbled by N_2 gas (0.2 liter/min) for 10 min, and 1 ml of these purged filtrates was placed in 10 ml of Aquasol (New England Nuclear) for counting. Activities of ^{14}C were estimated by a Beckman LS-133 liquid scintillation counter.

Irradiance by wavelengths from 0.3 to 3 μm was measured by a Star Pyranometer connected to a strip chart recorder at the University of Victoria, approximately 22 km from the station in Saanich Inlet. These measurements were reduced by 50% to give photosynthetically active irradiances. These values were reduced by 10% on clear and by 7% on overcast days to account for reflections from the sea surface (Jerlov 1968). Subsurface irradiances were measured by a Kahlsico Submarine Photometer (Model No. 268WA310) fitted with a clear filter.

Concentrations of nitrite and nitrate ions were determined by methods outlined in Bendschneider and Robinson (1952), and in Morris and Riley (1963) with ammonium chloride as a column activator (Grasshoff 1964), and with cadmium–copper columns (Wood et al. 1967), respectively.

Theoretical activities of ^{14}C in phytoplankton populations when cells become saturated with ^{14}C can be determined by the equation:

$$A = T \cdot S \frac{^{14}C}{^{12}C} \qquad (8)$$

where A is activity (dpm), T is a constant of 0.991×10^7 dpm $(\mu g\ ^{14}C)^{-1}$, S is phytoplankton carbon (μg/liter), ^{14}C is the inorganic pool of carbon-14 (μCi/liter), and ^{12}C is the inorganic pool of carbon-12 (μg/liter). Differential rates of ^{14}C and ^{12}C transport across cell membranes (Park and Epstein 1960) were ignored.

Results

Theoretical activities in phytoplankton populations were compared to actual ^{14}C activities measured in populations with depth and with season (Fig. 3 and 4). These comparisons were complex; however, one important observation emerged. Theoretical activities based on microscopy and

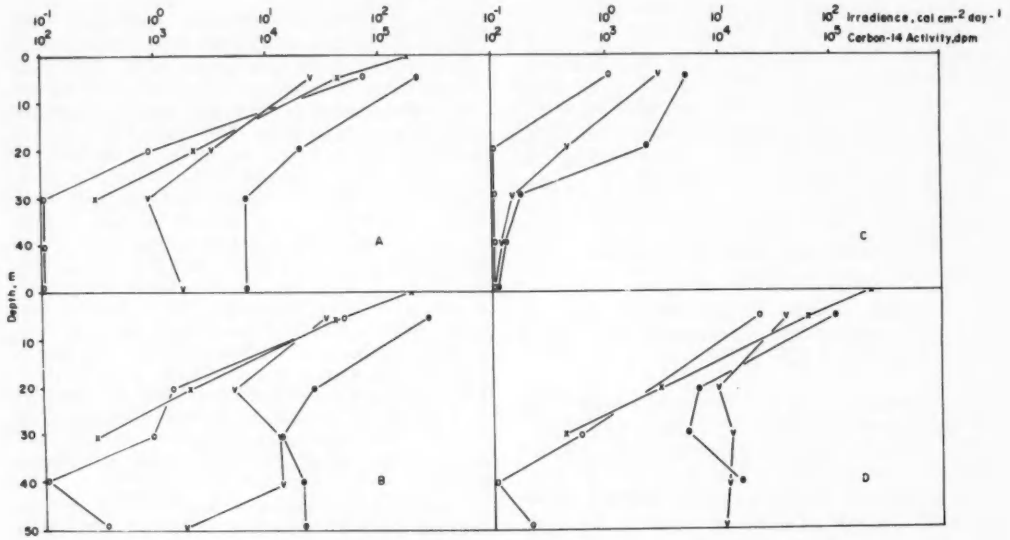

FIG. 3. Vertical distributions of irradiance (X), primary productivity (O), estimated minimum ^{14}C activity to estimate net primary productivity based on phytoplankton carbon (V), and on chlorophyll *a* (●) during A, March 21–22; B, April 4–5; C, April 18–19; and D, May 9–10.

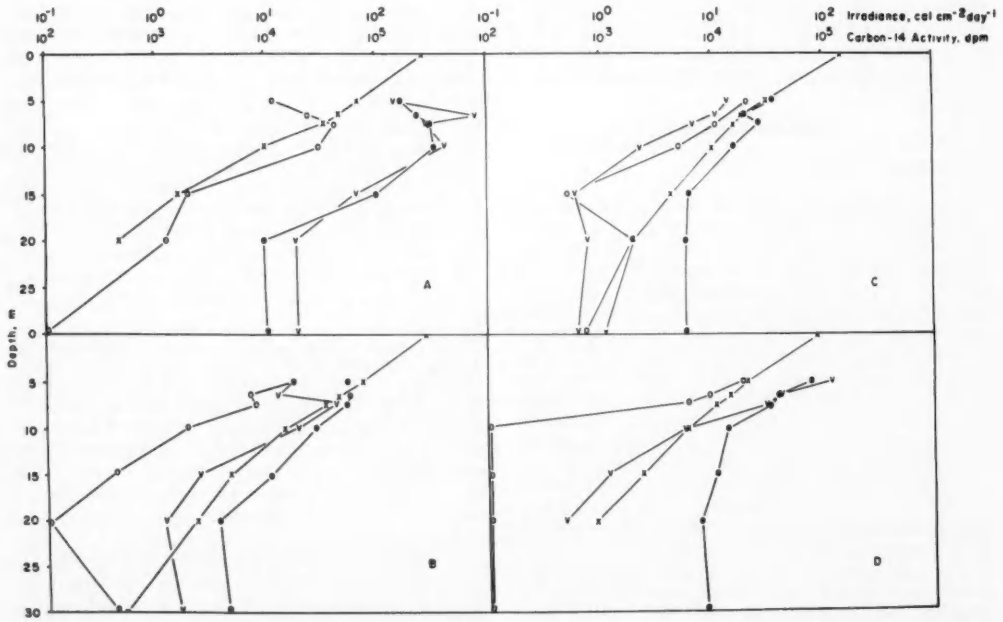

FIG. 4. Vertical distributions of irradiance (X), primary productivity (O), estimated minimum ^{14}C activity to estimate net primary productivity based on phytoplankton carbon (V), and on chlorophyll *a* (●) during A, May 30–31; B, June 21–22; C, September 27–28; and D, October 24–25.

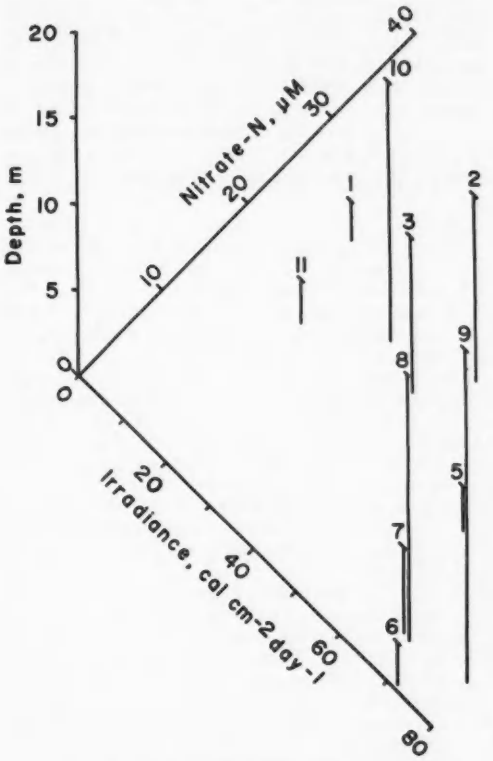

FIG. 5. Depths below which saturation of crops did not occur, NO_3-N concentrations, and irradiance at 5 m during cruise No. 1) February 28–March 1; 2) March 21–22; 3) April 4–5; 4) data incomplete; 5) May 9–10; 6) May 30–31; 7) June 21–22; 8) July 12–13; 9) August 1–2; 10) September 27–28; and 11) October 24–25. A depth of 2.5 m was arbitrarily selected when net primary productivity was not measured at 5 m.

on chlorophyll *a* frequently were greater than measured activities. This result could be due to either overestimation of phytoplankton carbon by our techniques or to disequilibrium of ratios of ^{14}C:^{12}C outside and inside cells. Our theoretical studies support the latter interpretation which indicates that saturation of crops with ^{14}C did not occur at depths greater than 15 m, a depth shallower than the depth of the 1% isolume, except in late May. At depths shallower than 15 m, saturation of crops occasionally occurred. Depths below which saturation of crops did not occur were compared to subsurface irradiations and nitrate concentrations (Fig. 5). Saturation of crops did not occur at depths of 5 m or greater twice when irradiations at 5 m were less than

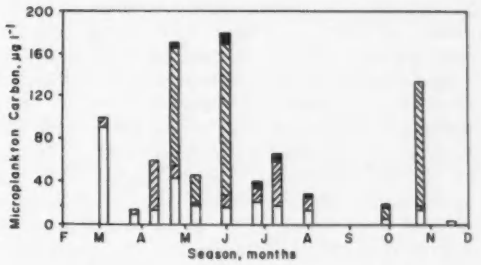

FIG. 6. Seasonal variation of microplankton carbon (■ dinoflagellates, ▨ diatoms, ▨ ciliates, □ μ-flagellates) at 5 m.

20 cal cm^{-2} day^{-1} and once when NO_3-N concentrations at 5 m were less than 2 μM. One observation indicated that saturation did not occur at 5 m when irradiation at 5 m was about 60 cal cm−2 day^{-1} and NO_3-N was about 12 μM. Timing of these saturations did not appear to be related to taxonomic composition of phytoplankton crops (Fig. 6). Phytoplankton carbon was dominated by diatoms during spring (April–June) and fall (September–October) blooms, μ-flagellates and dinoflagellates from June to September, and μ-flagellates during November and March. Excretion of labeled organic compounds by these populations was not detected by our methods.

Discussion and Conclusions

Results of our theoretical study suggest that the ^{14}C technique only measures net production when cells are exposed to optimal irradiation for periods exceeding about 30 h; results of our field study suggest that the ^{14}C technique only measures net production when cells are exposed to optimal irradiation and nutrient concentrations in 24-h experiments. Two potential sources of systematic error in our field study make our estimates of ^{14}C in populations of cells low and the frequency of measurement of net primary production may be overestimated. These errors are: 1) ratios of carbon to chlorophyll *a* were usually less than 25 and frequently less than 10, and these appear to be too low when compared to other studies (e.g. Hobson and Ketcham 1974; Hobson et al. 1973). These low ratios could be produced by overlooking parts of phytoplankton crops with the inverted microscope, giving low estimates of phytoplankton carbon in equation (8); and 2) during an experiment, ^{12}C and ^{14}C accumulate in phytoplankton cells and ^{12}C accumulation was ignored in our field studies. Inclusion of increases in ^{12}C would increase the amount of ^{14}C required

to saturate cells. Thus, during summer in temperate latitudes, an experiment carried out to measure net production should be for about 48 h. These conclusions do not agree with experimental observations by Bunt (1965) and Ryther and Menzel (1965) and with field observations by Antia et al. (1963) and McAllister et al. (1961), all of which indicate that net productivity of phytoplankton is measured by the ^{14}C technique in 24-h experiments. This disagreement can be explained if one assumes that net and gross photosynthetic rates were similar in their experimental and field studies. Clearly, direct measurement of respiration and photorespiration rates in phytoplankton populations needs to be made to further evaluate the ^{14}C technique.

When cells are exposed to conditions that produce low values of gross photosynthesis and respiration and when these values are low and similar, the theoretical model predicts that many hours are required for saturation of cell carbon with ^{14}C. However, if newly synthesized labeled substrates are preferentially decarboxylated, then the time required for net photosynthesis to be measured decreases. The magnitude of this decrease depends on the size of the pool of substrate that is preferentially used and the exchange rate between this pool and total cell carbon. Further theoretical and biochemical studies are required to determine the effects of pool size and exchange rate on our interpretation of the ^{14}C technique.

Integration of primary production over depth must produce overestimates of net primary production per unit sea surface. This overestimation could be serious in temperate latitudes during summer when nutrient limitation of photosynthesis may occur. In tropical latitudes, net primary production might be overestimated near the sea surface where light inhibition and nutrient limitation occur. Again, magnitude of these overestimations must depend on respiration and photorespiration rates in the phytoplankton. If rates are large, then errors in estimation will be large and vice versa.

Estimates of phytoplankton carbon before measurements of primary productivity could be used to estimate minimum activities required to saturate crops. Also, estimates of gross photosynthetic rates by very short exposures of crops to ^{14}C could be used to predict times required for crops to reach saturation. Use of either of these methods would aid in understanding what the ^{14}C technique measures.

Acknowledgments

We thank the Ministry of Transport through the Canadian Committee on Oceanography for continued use of M.V. *Vancouver* II and the assistance of her former captain, D. R. Hartley. We also acknowledge the able technical assistance of D. E. Ketcham of Harmac Pulp Limited, Nanaimo, B.C., and mathematical assistance of H. Barclay of the University of Victoria. This research was supported by grants from the National Research Council of Canada and the Faculty Research Fund of the University of Victoria.

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Temperature Selection of Juvenile Atlantic Salmon (*Salmo salar*) as Influenced by Various Toxic Substances

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PETERSON, R. H. 1976. Temperature selection of juvenile Atlantic salmon (*Salmo salar*) as influenced by various toxic substances. J. Fish. Res. Board Can. 33: 1722–1730.

Previous exposure to sodium pentachlorophenate (NaPCP), Guthion®, malathion, Dursban®, and Dibrom® lowered the preferred temperature for juvenile Atlantic salmon (*Salmo salar*) tested in a horizontal temperature gradient. Lindane, $CuSO_4$, $ZnSO_4$, $CdSO_4$, Sevin®, heptachlor, and fenitrothion did not change the preferred temperature significantly. Comparison with other published results indicates that those substances that increase the preferred temperature are more toxic (based on relevant changes in 24-h LC50) at low temperatures and vice versa. It is suggested that such shifts in selected temperature may be of potential immediate, short-term, survival value to the fish.

PETERSON, R. H. 1976. Temperature selection of juvenile Atlantic salmon (*Salmo salar*) as influenced by various toxic substances. J. Fish. Res. Board Can. 33: 1722–1730.

Une exposition préalable au pentachlorophénate de sodium (NaPCP), au Guthion®, au malathion, au Dursban® et au Dibrom® abaissent la température préférée de jeunes saumons atlantiques (*Salmo salar*) soumis à des essais dans un gradient de température horizontal. La lindane, le $CuSO_4$, le $ZnSO_4$, le $CdSO_4$, le Sevin®, l'heptachlore et le fénitrothion ne changent pas la température préférée de façon significative. Si l'on compare avec d'autres résultats publiés, on constate que les substances qui élèvent la température préférée sont plus toxiques (sur la base de changements dans la CL_{50} après 24 h) à de basses températures et vice versa. De tels changements dans le choix de la température pourraient favoriser, dans l'immédiat et à court terme, la survie du poisson.

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THE importance of temperature as a factor controlling many aspects of fish physiology and behavior has been much investigated and reviewed (Prosser and Brown 1961; Fry 1967). Thermal preference behavior has been demonstrated many times in the laboratory (Doudoroff 1938; Sullivan and Fisher 1953, 1954). Similarly, temperature may limit distribution in the environment because a species may confine its activities to certain regions of natural temperature gradients.

Several toxic substances at sublethal concentrations have an influence on the temperature selected by fish in the laboratory. Among these are chlorinated hydrocarbons of the DDT group (Ogilvie and Anderson 1965; Peterson 1973a), KCN (Anderson 1971), aldrin (Peterson 1973a), and $CuSO_4$ (Opuszýnski 1971). The influences of 12 toxic substances, from 3 chemically distinct groups, on the thermal preference of juvenile Atlantic salmon (*Salmo salar*) are presented here. These results and those of previous investigations on altered preferred temperature are discussed in relation to potential survival value and compared to determine whether all toxic substances seem to affect thermal preference and whether various classes of substances follow recognizable patterns.

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Materials and Methods

GRADIENT

A horizontal temperature gradient, described fully by Peterson (1973a), was used in all experiments. Briefly it consisted of a 1.3-cm aluminum plate, 1.9 × 1.7 m, divided longitudinally into 8 channels, each 16.2 cm wide. Each channel was marked off in 14 divisions for purposes of recording locations of fish. Thus, up to 8 groups of 5 fish were tested simultaneously. Water at 3.0–4.0 C flowed into each of the 8 channels at 100 ml/min, and was heated linearly to 26.0 C at the outflow end. Water depth was 1.5 cm.

PURITY OF COMPOUNDS

The heavy metal salts were standard reagent grade chemicals. The pesticides, with the exception of fenitrothion, were a minimum of 95% purity (obtained from Chem Service). The fenitrothion, a Bayer

TABLE 1. Toxicants and carriers (solvents) used in preferred temperature studies with juvenile Atlantic salmon (*Salmo salar*) including the amounts of carriers added to 10 liters of water in test and control situations. For the heavy metals, Na_2SO_4 was added to control vessels to provide equal SO_4^{2-} concentration in control solutions. (NaPCP = sodium pentachlorophenate.)

Toxicant	Carrier	Control carrier amount in 10 liters of test solution
NaPCP	Acetone	1 ml
Sevin®	"	"
Lindane	"	"
Dursban®	"	"
Dibrom®	"	"
Heptachlor	"	"
Malathion	"	"
Fenitrothion	Corexit® 7664	1 mg
Guthion®	"	"
$CuSO_4$	H_2O	Na_2SO_4
$ZnSO_4$	"	"
$CdSO_4$	"	"

product, was obtained from Forest Protection Ltd., Fredericton, N.B. It contained several impurities (Zitko and Cunningham 1974).

Dosing of Fish

Atlantic salmon tested were 3.0–4.0 cm body length and were acclimated to 15.0 C for at least 3 wk prior to use. Fish were exposed to the concentrations of the various chemicals for 24 h in 10 liters of solution in jars held at the acclimation temperature. Carriers for the toxicants and the treatments for corresponding control groups are given in Table 1. For a discussion of the toxicity of acetone and Corexit® 7664, see Peterson (1973a). Salmon used in the experiments averaged 1 g in wt, and no more than 18 (usually 15) were placed in a single jar. Hence the ratio of fish weight (grams) to water volume (liters) never exceeded 2. At the end of the 24-h exposure period the fish were transferred to the gradient in groups of 5 where they were left for 1 h before observations were begun. At least 1 control group, and usually 2 were tested simultaneously with the pretreated fish. All experiments on any given chemical were completed within a 2-wk period. As a result, no temporal bias was observed for any of the control groups, although different control groups for the various chemicals yielded fluctuations which could be attributed to seasonal effects, or perhaps in some cases to different stocks of fish.

Accumulation and Analysis of Data

The position of each fish in the gradient was recorded at 2-min intervals for 64 min. Cumulative data for each group of 5 fish were plotted to obtain a curve showing the frequency with which fish were observed in the various subdivisions. The arithmetic mean of the distribution was used as the measure of central tendency. Skewness did not appear to introduce significant error in any of the experiments. For a more complete discussion of the data analysis, see Peterson (1973a, b).

Q_{TOX} — its Definition and Calculation

Previous publications on the effects of temperature on toxicity of various substances to fish are utilized by standardizing the results as follows: 1) Species closely related to Atlantic salmon are used where possible (usually rainbow trout, *Salmo gairdneri*). Sources of data used are contained in Table 2. 2) The 24-h LC50 is the parameter of toxicity most frequently published and is used here for estimation of temperature effects on toxicity. 3) The temperature ranges used differ in different papers, and an adaptation of the Q_{10} formula has been used to standardize results. For want of a better term, and to be consistent with the term "Q_{10}", the term "Q_{TOX}" or "temperature quotient of toxicity" is used in this paper. The formula is:

$$Q_{TOX} = \left[\frac{LC50\ (at\ T_2)}{LC50\ (at\ T_1)}\right]^{\frac{10}{T_1 - T_2}}$$

where $T_1 > T_2$; LC50 = 24-h LC50; T = temperature (C). This formula converts the data to the quotient of the LC50s at temperatures 10 C apart. A $Q_{TOX} < 1$ indicates greater toxicity at lower temperatures and vice versa. For a Q_{TOX} of 2, the LC50 is halved for every 10 C increase (i.e. the toxicity is doubled). Likewise for a Q_{TOX} of 0.5, the LC50 is doubled for every 10 C increase (toxicity halved). Where the 24-h LC50s are given at more than two temperatures, the Q_{TOX} is calculated for the two extremes. The rationale for this is that, in most cases, insufficient points were available to determine the true nature of the curve relating LC50 to temperature.

Results and Discussion of Specific Groups of Toxic Chemicals

In this section the data are organized according to the various classes of chemicals investigated. For each class of chemicals, new data will be presented first, followed by a brief review of previously published data on the influence of these chemicals on temperature selection and of data utilized here in calculation of Q_{TOX} values.

Organochlorines

When juvenile Atlantic salmon pretreated with NaPCP were placed in the gradient, convulsions were elicited upon movement into the lower temperatures (4.0–7.0 C) — similar to the behavior of DDT-treated fish (Peterson 1973a). This similarity did not carry over into the results

TABLE 2. Effects of temperature on toxicity of various chemicals (expressed as "Q_{TOX}") and the influences of these chemicals on preferred temperature (+, indicates increase in preferred temperature, −, indicates a decrease). Concentrations listed are those giving the maximum effect on preferred temperature. (NaPCP = sodium pentachlorophenate.)

Chemical	Concn (*ppm*)	Change in preferred temp (*C*)	Source	Q_{TOX}	Source
Organochlorines					
pp′DDT	0.03–0.05	+(4–5) (*Salmo salar*)	Ogilvie and Anderson (1965) Peterson (1973a)	0.7 (*Salmo gairdneri*)	Cope (1964)
op′DDT	0.16–0.30	+(4–5) "	" "	—	—
pp′DDD	0.04–0.10	+(4–5) "	" "	—	—
pp′DDE	0.50–2.00	+(4–5) "	" "	—	—
methoxychlor	0.04–0.05	+(4–5) "	" "	0.7 "	Cope (1964)
aldrin	0.05–0.15	−3 "	" "	2.6 "	Macek et al. (1969)
dieldrin	0.01–0.025	−1(N.S.) "	Peterson (1973b)	3.6 "	" " "
heptachlor	0.005–0.025	−(1–1.5)(N.S.) "	Fig. 1A	1.3 "	" " " "
lindane	0.01–0.03	+1(N.S.) "	Fig. 1B	1.2 (*Lepomis macrochirus*)	Cope (1964), Macek et al. (1969)
NaPCP	0.05–0.10	−5 "	Fig. 1C	0.8 (*S. salar*)	This paper
Aroclor® 1254	2	0 "	Peterson (1973a)	—	—
"	25–100	0(*Salvelinus fontinalis*)	Miller and Ogilvie (1975)	—	—
Organophosphates					
azinphosphorethyl (Guthion)®	0.002–0.003	−4 (*Salmo salar*)	Fig. 1D	1.8 (*S. gairdneri*)	Macek et al. (1969)
malathion	0.025–0.050	−2 "	Fig. 1E	0.8 "	Cope (1964)
—	—	—	—	1.9 (*L. macrochirus*)	Macek et al. (1969)
fenitrothion	0.30–1.00	−2(N.S.) "	Fig. 1F	—	—
chlorpyrifos (Dursban®)	0.10–0.25	−4 "	Fig. 2A	7.9 (*S. gairdneri*)	Macek et al. (1969)
naled (Dibrom®)	0.15–0.30	−4 "	Fig. 2B	4.6 "	Macek et al. (1969)
Heavy metals					
$CuSO_4$	0.015–0.030	−2(N.S.) "	Fig. 2C	—	—
$ZnSO_4$	0.20–0.25	−5(*Pimephales promelas*)	Opuszyński (1971)	—	—
	0.4	0 (*S. salar*)	Fig. 2D	1.9 (*S. gairdneri*)	Lloyd and Herbert (1962)
				(*S. salar*)	Hodson and Sprague (1975)
$CdSO_4$	0.002	−1(N.S.) (*S. salar*)	Fig. 2E	—	—
Miscellaneous					
KCN	0.02–0.04	−5 "	Anderson (1971)	3.8 (*Gillichthys*)	Sumner and Doudoroff (1938)
carbaryl (Sevin®)	0.25–1.00	0 "	Fig. 2F	—	—
phenol	10	−3(*Salvelinus fontinalis*)	Miller and Ogilvie (1975)	0.4 (*S. gairdneri*)	Brown et al. (1967)

obtained for selected temperature. Two sets of experiments (performed in 1973 and 1974) (Fig. 1C) indicate a decreasing selected temperature after exposure to increasing concentrations of NaPCP. The maximal decrease is 3.0–4.0 C. Estimates of 24-h LC50s for NaPCP at different temperatures were not available. Alderdice (1963) found median mortality times for coho salmon (*Oncorhynchus kisutch*) to be shorter at higher temperatures (13.0 vs. 5.0 C), but used concentrations much higher than the 24-h LC50. In a series of running water toxicity tests conducted by the author, the 24-h LC50s were estimated at 0.90, 0.105, and 0.118 ppm at 10.0, 15.0, and 20.0 C, respectively for 15.0 C-acclimated Atlantic salmon. The 10.0 C-LC50 was significantly lower than the 20.0 C-LC50 ($P < 0.05$). These values yield a Q_{TOX} of 0.8. Although the effects of temperature on NaPCP toxicity remain somewhat equivocal, a Q_{TOX} of 0.8 is accepted for the present.

Preexposure to lindane did not influence significantly the preferred temperature of salmon alevins (Fig. 1B). The pooled treatment mean was 1.0 C higher than the control mean.

Preexposure to heptachlor (Fig. 1A) resulted in a slight lowering of selected temperature with differences between individual treatments and controls not differing significantly. If all the heptachlor treatments were pooled, then the pooled treatment mean did differ significantly from the control mean ($t = 2.35$, $P < 0.05$).

Ogilvie and Anderson (1965) and Peterson (1973a) demonstrated that after exposure to the compounds of the DDT group (*pp*′DDT, *op*′DDT, *pp*′DDD, *pp*′DDE, and methoxychlor) at one-fifth the 24-h LC50 or greater, juvenile Atlantic salmon selected temperatures 4.0–5.0 C higher than did controls. After exposure to doses of this level they also exhibit the symptoms of acute DDT poisoning — convulsive seizure at low temperatures. The Q_{TOX} of 0.7 for *pp*′DDT (7.2–18.3 C) and methoxychlor (1.6–12.7 C) indicates greater toxicity at lower temperatures (Table 2). A similar value was calculated from methoxychlor toxicity data published for the bluegill (*Lepomis macrochirus*) (Macek et al. 1969). Preexposure for 24 h to concentrations one-twentieth the 24-h LC50 induces a lower preferred temperature in juvenile salmon (Anderson 1971). Since this effect does not appear to be associated with acutely toxic doses, it will not be discussed further in this paper.

After exposure to compounds of the aldrin group, juvenile Atlantic salmon usually selected lower temperature than did controls. This effect

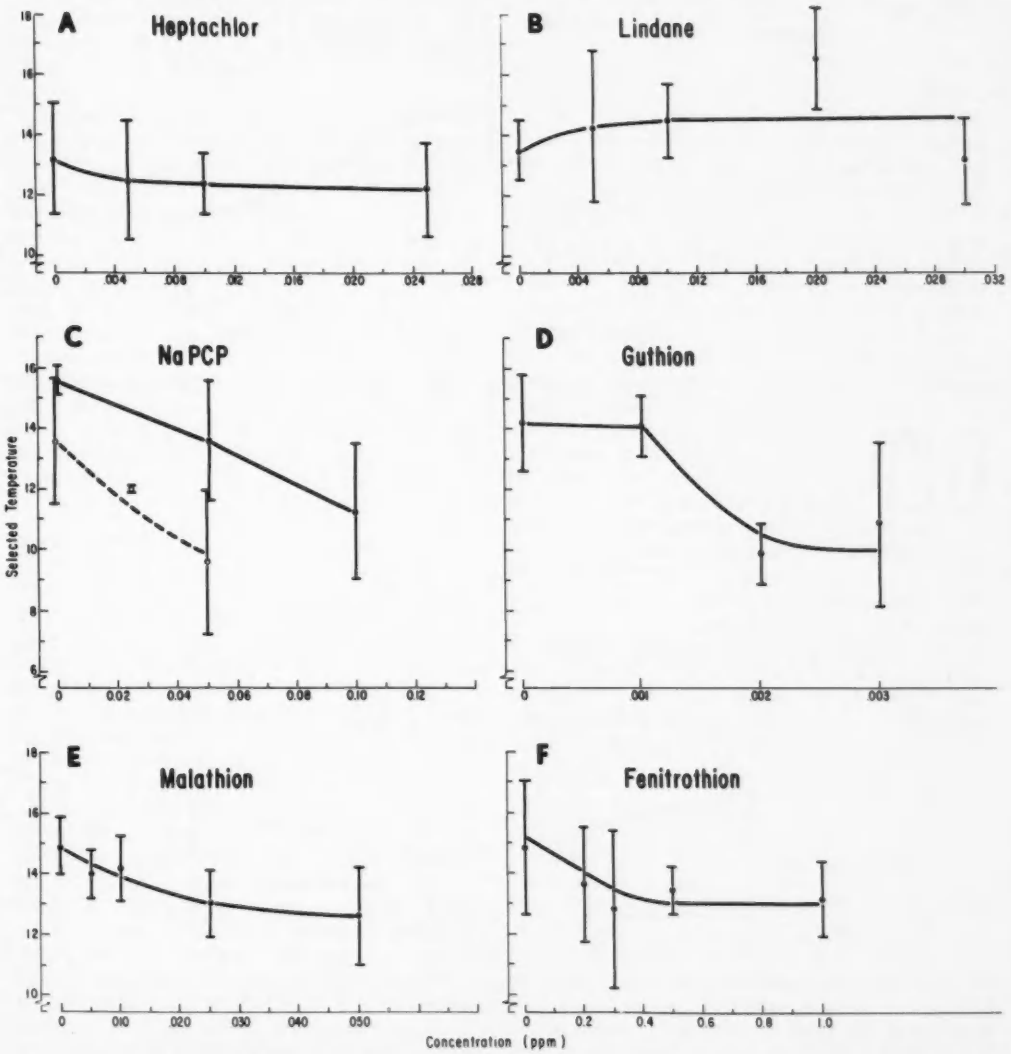

FIG. 1. Selected temperature of juvenile Atlantic salmon (*Salmo salar*) in groups of five in a horizontal gradient as a function of a concentration of test substance to which they were previously exposed for 24 h. Bars indicate ± 1 SD. Number of experiments performed for each point, reading from left to right on each curve, are: A, 10, 6, 6, 8; B, 9, 2, 4, 8, 7; C, 1973 (solid line) — 4, 6, 7; 1974 (dotted line) — 6, 2, 3; D, 12, 4, 6, 6; E, 12, 4, 6, 6, 5; F, 14, 3, 6, 6. Percent mortalities at the highest concentration of each substance: A, 0 (90% at 50 ppb); B, 30; C, 15; D, 7; E, 25; F, 20.

was slight for dieldrin (Peterson 1973b) (Table 2) and heptachlor (Fig. 1A). The Q_{TOX}'s (1.6–12.7 C) for aldrin and dieldrin are 2.6 and 3.6, respectively, indicating that the compounds are more toxic at higher temperatures (Table 2). Heptachlor seems to be only slightly more toxic at higher temperatures with a Q_{TOX} of 1.3 (1.6–12.7 C).

Temperature has little effect on the lindane 24-h LC50. Q_{TOX} values of 1.0 and 1.3 were calculated for the bluegill (Table 2, these two values averaged).

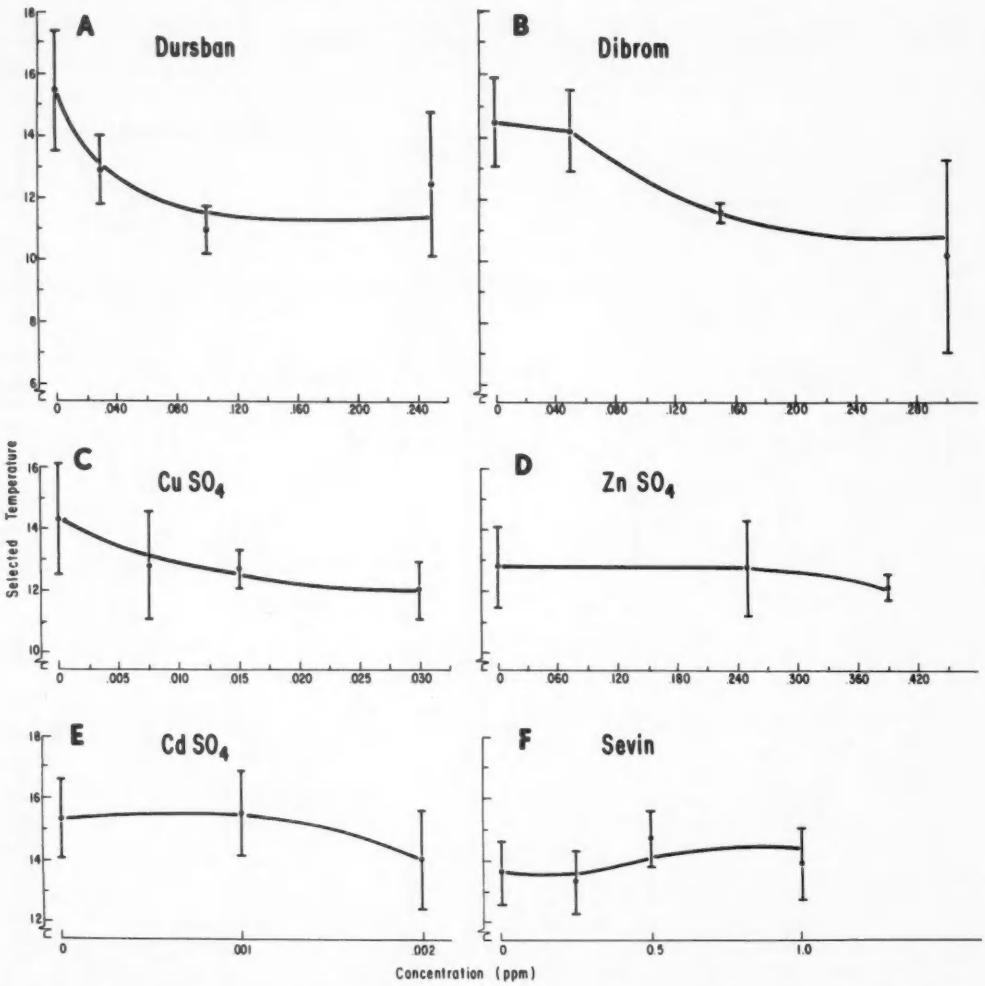

FIG. 2. Selected temperature of juvenile Atlantic salmon in a horizontal gradient as a function of concentration of test substance to which they were previously exposed for 24 h. Bars indicate ± 1 SD. Number of experiments performed for each point, reading from left to right on each curve are: A, 12, 6, 6, 5; B, 7, 6, 6, 4; C, 6, 6, 6, 6; D, 6, 5, 5; E, 8, 5, 6; F, 6, 6, 5, 6. Percent mortalities at the highest concentration of each substance: A, 40; B, 40; C, 10; D, 23; E, 3; F, 6.

Peterson's (1973a) finding that preexposure to 2 ppm Aroclor® 1254 did not influence the selected temperature of salmon has been confirmed and extended by Miller and Ogilvie (1975). No data are available on the effects of temperature on toxicity of PCB compounds to teleosts.

ORGANOPHOSPHATES

Preexposure to Guthion® (Fig. 1D) and malathion (Fig. 1E) lowered the selcted temperature (of juvenile Atlantic salmon) by 4.0 C ($P < 0.001$) and 2.0 C ($P < 0.05$), respectively. The selected temperature was also lowered by 2.0 C following exposure to 0.2–1.0 ppm fenitrothion (Fig. 1F), but the effect was not statistically significant. Peterson (1973b) also reported a slight lowering (ca. 1.0 C) of selected temperature by brook trout (*Salvelinus fontinalis*) in a vertical gradient following 24-h exposure to 0.5 ppm fenitrothion.

The selected temperature of juvenile Atlantic

salmon after exposure to adequate concentrations of Dursban® (Fig. 2A) and Dibrom® (Fig. 2B) was about 4.0 C lower than that of controls ($P < 0.01$ for Dursban®, $P < 0.001$ for Dibrom®).

Guthion® is more toxic at higher temperature with a Q_{TOX} of 1.8. The reported effects of temperature on malathion toxicity are complex (Cope 1964). The 24-h LC50 at 12.8 C was less than that of 7.2 C (0.085 ppm vs. 0.10 ppm) for rainbow trout. At 18.3 C the LC50 went up again to 0.13 ppm. The overall Q_{TOX} was 0.8. Macek et al. (1969) reported malathion to be more toxic to bluegills at higher temperatures with a Q_{TOX} of 1.9. The Q_{TOX} of 0.8 calculated from the rainbow trout data will be used in this paper. No data on the effects of temperature on fenitrothion toxicity were available. Temperature has a marked effect on the toxicity of both Dursban® and Dibrom®, a Q_{TOX} of 7.9 for the former and a Q_{TOX} of 4.6 for the latter (Table 2).

Heavy Metals

Juvenile Atlantic salmon did not show significant differences in selected temperature after exposure to the heavy metals $CuSO_4$ (Fig. 2C), $ZnSO_4$ (Fig. 2D), and $CdSO_4$ (Fig. 2E), although a trend toward a lowered preferred temperature is indicated. Opuszýnski (1971) found that previous exposure to copper markedly shifted the selected temperature of the fathead minnow (*Pimephales promelas*) downwards.

No data on the effects of temperature on copper toxicity to fish have been found. McLeese (1974) found that lobsters have longer resistance times to copper at low temperatures, but no change in threshold. Lloyd and Herbert (1962) found the toxicity of zinc to rainbow trout to be greater at higher temperatures, with a Q_{TOX} of 1.8 (13.5–21.5 C). Hodson and Sprague (1975) obtained results in general agreement with those of Lloyd and Herbert (1962). For fish acclimated to 11.0 C the average Q_{TOX} was 2.4, while for fish acclimated to 19.0 C a Q_{TOX} of 1.8 was obtained over the range 11.0–19.0 C. However, the toxicity increased again at 3.0 C for 19.0 C-acclimated salmon with a Q_{TOX} of 0.3 for 3.0–11.0 C. This last effect may be due to low temperature becoming a lethal factor and being additive with Zn^{++} in this instance. A Q_{TOX} of 1.9 has been assumed typical for zinc 24-h LC50s, since this is the average for salmon of all acclimations at test temperatures which were not stressful. No information has been found on the influence of temperature on toxicity of Cd^{++} to fish, although O'Hara (1973) reported Cd^{++} to be much more toxic to fiddler crabs at higher temperatures.

Miscellaneous Substances

The only carbamate pesticide tested was Sevin®. No significant effect on selected temperature was obtained (Fig. 2F), nor have data been found on the effects of temperature on its toxicity.

Javaid (1967, reported in Anderson [1971]) found KCN to have a marked effect on the temperature selection of 10.0 C-acclimated Atlantic salmon. Fish pretreated with 0.02–0.04 ppm KCN selected 6.0 C compared with 11.5 C for controls. Several studies have been published on the toxicity of KCN to teleosts; however, most deal with resistance times shorter than 24 h. Sumner and Doudoroff (1938) found the resistance time of *Gillichthys* sp. to be shorter at higher temperatures, ranging from 40 min at 30.0 C to 5 h at 10.0 C for exposure to 0.001 M. A Q_{TOX} of 3.8 was calculated from their data. In the absence of other evidence, it is assumed that the temperature relationship for 24-h LC50s is similar.

Brown et al. (1967) found phenol to be more toxic to rainbow trout at lower temperatures, resembling DDT and methoxychlor in this respect. The Q_{TOX} for the 48-h LC50 was calculated to be 0.4. Miller and Ogilvie (1975) report that exposure to brook trout (*S. fontinalis*) to phenol at 10 ppm lowered the selected temperature by 3.0 C.

General Discussion

Many reports in the literature touch on the interaction between toxicities of various substances and temperature, and the subject has been recently reviewed (Cairns et al. 1975). However, with one exception — for zinc (Hodson and Sprague 1975) — none explicitly describes all the experimental conditions. In many it is not stated clearly whether fish were fully acclimated to the test temperatures. As a consequence, the relationship between the temperature dependence of toxicity and the duration of the test (or concentration of toxicant) is not clear for most toxic substances. However, the available evidence does suggest that the temperature dependence of toxicity is greater for high concentrations (i.e. short test durations and greater mortality rates). This fact is mentioned for several toxicants in the review by Cairns et al. (1975). In support of this suggestion, if one compares the ratios of the Q_{TOX} values for 96-h LC50s and 24-h LC50s as obtained from various sources (Table 3), one can see that the Q_{TOX} (and therefore the

TABLE 3. The ratios of Q_{TOX} for 96-h LC50 to the Q_{TOX} for 24-h LC50 for various chemicals.

Chemical	Ratio 96-h Q_{TOX}:24-h Q_{TOX}	Source
Methoxychlor	0.79	Macek et al. (1969)
*pp'*DDT	1.00	Cope (1964)
Malathion	0.91	Macek et al. (1969)
$ZnSO_4$	0.20	Hodson and Sprague (1975)
KCN	0.32	Sumner and Doudoroff (1938)
Heptachlor	0.83	Macek et al. (1969)
Guthion®	0.67	" " " "
Aldrin	0.53	" " " "
Dieldrin	0.38	" " " "
Dibrom®	0.43	" " " "
Dursban®	0.74	" " " "

temperature dependence) for the 96-h LC50s are always lower than the 24-h LC50s except *pp'*DDT where they are identical. The mean ratio is 0.6. In addition, the data of Hodson and Sprague (1975) indicate that at high zinc concentrations (ca. 30 ppm), irrespective of acclimation temperature, the rate of mortality is higher, the higher the temperature. As concentration is decreased, the median mortality times at the various temperatures tend to converge and usually intersect somewhere between 10 and 100 h.

Threshold levels in the data of Hodson and Sprague show a complex relationship to temperature, and acclimation temperature is apparently more important than test temperatures in determining thresholds. Threshold levels of several other substances have also been observed not to be temperature-dependent or to have complex relationships with temperature.

Mortality rates at high concentrations are probably highly temperature-dependent due to higher metabolic rate, hence greater rate of uptake of the toxicant at high temperatures (Hodson and Sprague 1975; Cairns et al. 1975). This postulation is also supported from Q_{TOX} values calculated from the data of Hodson and Sprague (1975). The Q_{TOX} for exposure to 30 ppm zinc is 5.1 for 3.0 C-acclimated salmon, 3.1 for 11.0 C-acclimated fish, and 2.0 for 19.0 C-acclimated fish. This is the order expected if Q_{TOX} magnitude reflects the involvement of differences in metabolic rates, since salmon acclimated to lower temperatures have higher metabolic rates and are more active at any given temperature (Peterson and Anderson 1969).

What then is the relationship, if any, between the effect of a toxic chemical on thermal preference and the temperature-dependence on the chemical's toxicity? Since the 24-h LC50 is the parameter of toxicity for which temperature characteristics are known for the widest variety of substances, the shifts in the selected temperatures are compared with the Q_{TOX} of the 24-h LC50 (Fig. 3) for the various substances cataloged in the previous section of the paper. Several compounds that are more toxic at low temperatures ($Q_{TOX} < 1$, e.g. *pp'*DDT, methoxychlor) induce an upward shift in selected temperature at near-toxic levels. Conversely, most compounds that are more acutely toxic at high temperatures ($Q_{TOX} > 1$) induce a shift to lower selected temperatures. While the effects of several of these compounds on selected temperature were not statistically different from the controls ($ZnSO_4$, heptachlor, $CdSO_4$, fenitrothion, dieldrin), they have been placed on the graph according to their nominal influence on selected temperatures. These differences in selected temperature are within 2.0 C of control values. Obviously, most of the compounds either do not influence selected temperature or lower it. Three compounds, malathion, NaPCP, and phenol, are most seriously out of alignment with the general trend, as indicated by the dashed line in Fig. 3. With the two former compounds, there is conflicting evidence for their temperature-dependence of toxicity. The Q_{TOX} for malathion and the bluegill was 1.9 (Table 2), putting it more in line with most of the other compounds, the Q_{TOX} of 0.8 from rainbow trout data (Cope 1964) is entered on Fig. 3 for comparison with salmon. The situation with NaPCP was discussed in the previous section. More work on this compound is probably desirable to determine what Q_{TOX} value is representative.

The organophosphates (Dursban®, Dibrom®, Guthion®, and malathion) in general have Q_{TOX}'s greater than 1.0, and may be nearly 8.0 in the case of Dursban®. They all lower the selected temperature or have little effect. Heavy metals fall into similar areas of the graph to the organo-

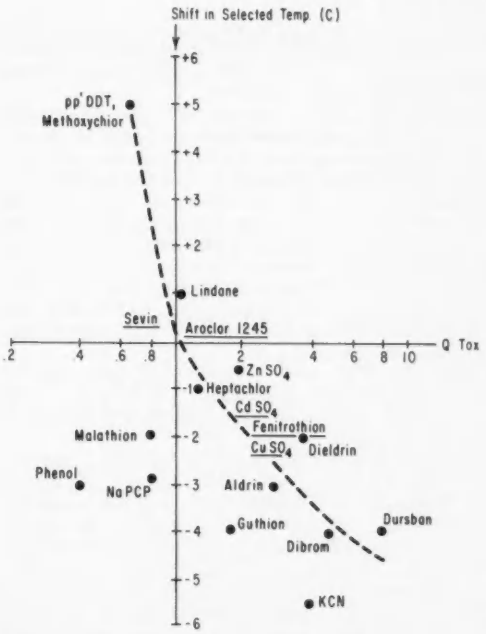

FIG. 3. Various substances discussed in the text are displayed according to the way they shift the selected temperature of juvenile Atlantic salmon (vertical axis), and the temperature dependence of the toxicity (horizontal axis, as calculated Q_{TOX}). See Materials and Methods for Q_{TOX} formula. Substances are underlined for which data on either selected temperature or toxicity are lacking, and are merely indicative of possible future location. See Discussion for more complete treatment.

phosphates, but responses appear to be more uniform within this group. The influence of heavy metals on temperature selection, on the average, is not as great as that of the organophosphates and most of the shifts lack statistical support.

Chlorinated hydrocarbons appear to fall into three groups. DDT-like compounds with Q_{TOX}'s less than 1.0 induce selection of higher temperatures. Compounds of the aldrin group (aldrin, dieldrin, and heptachlor) have a Q_{TOX} of 1.0 or more and induce selection of lower temperatures or have little effect. Lindane has no significant effect on temperature selection and the Q_{TOX} is near 1.0.

Several compounds for which the required information is incomplete are shown in Fig. 3 for whatever predictive value may be gained therefrom. Aroclor® 1245 and Sevin® have no significant effect on selected temperature, so the Q_{TOX} may lie near 1.0. Fenitrothion, judging from its nominal effect on preferred temperature, may have a Q_{TOX} near 2.

Most of the data summarized in Fig. 3 appear to fall in the lower right quadrant, with DDT-like compounds falling in the upper left. The scatter is considerable, which is not surprising considering the variety of experimental conditions and test organisms involved. The dashed line is meant only to indicate a general trend.

Assuming the relationships depicted in Fig. 3 are essentially correct, what are the environmental implications? Ferguson (1958), Smith and Saunders (1958), and Cherry et al. (1975) suggest that temperature selection can be a factor determining the distribution of fish in natural watersheds. Therefore, toxic substances that markedly affect thermal preference could also affect this distribution. It may also be postulated that shifts in preferred temperatures are of possible survival value in that, as a result of distributional changes in response to such shifts, the fish may move to an environment which is immediately less toxic. Such responses would appear to have the greatest potential survival value in cases where a slug of toxicant of relatively high concentration for a short duration is released into a stream. Possible long-term benefits to the fish are obscure because of the lack of data relating toxic threshold levels to temperature and because of the lack of data on the persistence of the effects of toxic substances on selected temperature. Perhaps the effects on selected temperature from long-term, chronic exposure of fish to toxicants would yield more meaningful relationships with corresponding toxicity thresholds than the short-term, high concentration exposures used in the experiments reported here.

Just how a fish is able to adjust its preferred temperature advantageously in the presence of toxic substances can only be conjectural. Shifts in preferred temperature cannot easily be related to shifts in overall metabolic rate as noted previously (Anderson 1971). For example, KCN depresses metabolism while NaPCP, an uncoupler, increases O_2 consumption (B. Holmberg and R. L. Saunders unpublished data), yet both induce a reduction in selected temperature. However, both substances tend to reduce cellular ATP levels, so perhaps the locus of the mechanism(s) lies in biochemical balance associated with ionic fluxes in the appropriate areas of the central nervous system. There is some evidence that such changes in ionic balance influence thermoregulation in mammals (Myers and Yaksh 1971) and temperature responses in crustacean temperature receptors (Shea et al. 1969).

Acknowledgments

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Long-Term Effects of Lead Exposure on Three Generations of Brook Trout (*Salvelinus fontinalis*)

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HOLCOMBE, G. W., D. A. BENOIT, E. N. LEONARD, AND J. M. MCKIM. 1976. Long-term effects of lead exposure on three generations of brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 1731–1741.

Exposure of three generations of brook trout (*Salvelinus fontinalis*) to mean total lead concentrations (0.9–474 μg/liter) showed that all second-generation trout exposed to 235 and 474 μg Pb/liter and 34% of those exposed to 119 μg Pb/liter developed severe spinal deformities (scoliosis). Scoliosis also appeared in 21% of the newly hatched third-generation alevins exposed to 119 μg Pb/liter, and weights of these fish 12 wk after hatch were significantly reduced. Gill, liver, and kidney tissues of first- and second-generation brook trout accumulated the greatest amount of lead. Only small amounts accumulated in the edible muscle. An equilibrium of lead residues was reached in liver and kidney tissue from second-generation fish after 70 wk of exposure, but not in gill tissue. Fish exposed to 119 μg Pb/liter and then placed in uncontaminated control water for 12 wk showed a 70, 78, and 74% loss in micrograms Pb per gram for gill, liver, and kidney tissue, respectively, and a 39, 56, and 35% loss, respectively, in the total micrograms of Pb in the whole tissue. Residue analysis of eggs, alevins, and juveniles showed that lead was accumulated during these life stages. The maximum acceptable toxicant concentration (MATC) for brook trout in water with a hardness of 44 mg/liter (as $CaCO_3$) and a pH of 6.8–7.6 lies between 58 and 119 μg/liter for total lead and between 39 and 84 μg/liter for dissolved lead. The MATC was based on the development of scoliosis in second- and third-generation fish and the reduced growth of 12-wk-old third-generation trout. The 96-h LC50 for brook trout was 4100 μg/liter based on total lead and 3362 μg/liter based on dissolved lead; therefore, the application factor (MATC/96-h LC50) lies between 0.012 and 0.029 for both total and dissolved lead.

HOLCOMBE, G. W., D. A. BENOIT, E. N. LEONARD, AND J. M. MCKIM. 1976. Long-term effects of lead exposure on three generations of brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 33: 1731–1741.

Après exposition de trois générations d'ombles de fontaine (*Salvelinus fontinalis*) à des concentrations totales moyennes de plomb (0.9–474 μg/litre), on constate que tous les ombles de deuxième génération exposés à 235 et 474 μg de Pb/litre et 34% de ceux exposés à 119 μg de Pb/litre manifestent de sérieuses déviations de la colonne vertébrale (scoliose). La scoliose apparaît également chez 21% des alevins de troisième génération nouvellement éclos exposés à 119 μg de Pb/litre; le poids de ces derniers est significativement moindre 12 semaines après éclosion. Les tissus des branchies, du foie et du rein des ombles de première et deuxième générations accumulent la plus grande quantité de plomb. Il ne s'accumule que de faibles quantités dans le muscle comestible. Un équilibre des résidus de plomb est atteint dans le tissu hépatique et rénal de poissons de deuxième génération après 70 semaines d'exposition, mais non dans le tissu branchial. Les poissons exposés à 119 μg de Pb/litre et ensuite placés dans une eau témoin non contaminée durant 12 semaines perdent 70, 78 et 74% en microgrammes Pb par gramme du tissu des branchies, du foie et du rein respectivement, et 39, 56 et 35% respectivement en microgrammes totaux de Pb pour le tissu entier. L'analyse des résidus dans les œufs, les alevins et les jeunes démontre que l'accumulation du plomb se produit à ces stades. La concentration toxique acceptable maximum (CTAM) pour l'omble de fontaine dans de l'eau d'une dureté de 44 mg/litre (sous forme de $CaCO_3$) et de pH de 6.8–7.6 se situe entre 58 et 119 μg/litre pour le plomb total et entre 39 et 84 μg/litre pour le plomb dissous. La CTAM est fondée sur le développement de la scoliose chez les poissons de deuxième et de troisième générations, et sur la croissance ralentie d'ombles de troisième génération âges de 12 semaines. La CL50 après 96 h pour l'omble de fontaine est de 4 100 μg/litre sur la base de plomb total et de 3 362 μg/litre sur la base de plomb dissous; cependant, le facteur d'application (CTAM/CL50 après 96 h) se situe entre 0.012 et 0.029 tant pour le plomb total que pour le plomb dissous.

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CONCENTRATIONS of lead are steadily increasing in rivers, lakes, and oceans (National Academy of Sciences 1972). Lead is a cumulative toxic metal that has no known beneficial or desirable nutritional effect on fish or other animals (McKee and Wolf 1963). Lead accumulates in the bones and tissues of fish and in high enough concentrations can cause anemia (Dawson 1935), impairment of the function of the liver, kidney, and spleen (Haider 1964), spinal deformities (Davies and Everhart 1973), and death (McKee and Wolf 1963).

Little information is available, however, on the chronic or long-term toxicity of lead to fish, other than the work of Davies and Everhart (1973) with rainbow trout, *Salmo gairdneri*. Some field survey investigations have been done on lead residues in fish carcasses (Pakkala et al. 1972) and on lead residues in trout tissues (Pagenkopf and Neuman 1974), but the concentrations of lead to which these fish were exposed were not known. No previous studies are available dealing with chronic lead toxicity to fish and residue accumulation involving several successive generations and all developmental stages.

This study was designed to determine the chronic effects of lead on survival, growth, and reproduction of three generations of brook trout (*Salvelinus fontinalis*) exposed over a 3-yr period, and to ascertain the accumulation rate, distribution, and dissipation of lead residues from the tissue of exposed trout. This work was also designed to determine the sensitivity of the various life stages of the brook trout to lead, to determine the maximum acceptable toxicant concentration (MATC), and to calculate an application factor for lead as described by Mount and Stephan (1967).

Materials and Methods

PHYSICAL AND CHEMICAL

Exposure system — The exposure system consisted of a proportional diluter (Mount and Brungs 1967) that delivered 2 liters of test water per cycle to flow-splitting chambers (Benoit and Puglisi 1973). These chambers divided each of the six diluter concentrations four ways into two duplicate adult spawning tanks and two duplicate larval growth tanks. Larval growth tanks were located directly above and drained into the adult spawning tanks of the same concentration. Test-water flow rates averaged 570 ml/min for the adult spawning tanks and 86 ml/min for the larval growth tanks. Replacement time for 90% of the test water was calculated to be approximately 5 h in the adult spawning tanks and larval growth chambers (Sprague 1969). Adult spawning tanks were 91 × 31 × 38-cm stainless steel tanks with a 31-cm standpipe. Larval rearing facilities consisted of an outer glass tank, 55 × 28 × 15 cm, with an inside tank, 43 × 26 × 15 cm, divided lengthwise into two 13-cm-wide growth chambers. Water depth in each chamber measured 13 cm. All tanks were gently aerated, siphoned Monday through Friday, and scrubbed once a week. All adult spawning tanks were covered with fiberglass mesh screens and concealed by curtains to minimize disturbance. Embryos and alevins up to 4 wk old were protected from direct light by black plastic covers and incubated in nearly complete darkness (0.02 lm). A combination of Sylvania Gro-Lux and Duro-Test Vita-Lite (the U.S. Environmental Protection Agency neither recommends nor endorses any commercial product; trade names are used only for identification) fluorescent lamps were used as the main source of illumination. Fluorescent lamps were used in conjunction with incandescent bulbs wired to a light timer which controlled the photoperiod and an automatic dimmer that simulated sunrise and sunset (Drummond and Dawson 1970). Maximum light intensity was 8.5 lm at the water surface of the adult spawning tanks.

Water characteristics — Water throughout the exposure was obtained directly from Lake Superior. It was passed through an ultraviolet sterilizer to kill >99% of possible pathogens and heated to the test temperature by a hot water heat-exchange system. Seasonally adjusted temperatures ranged from 9 to 15 C throughout the juvenile–adult exposures. Temperatures were maintained at 9 ± 1 C during all spawning, embryo-incubation, and 12-wk posthatch alevin–juvenile growth studies. Total hardness, alkalinity, acidity, and pH determinations were made on all tanks, alternately, one tank a week; dissolved oxygen was measured in a different tank twice a week. Means and range for total hardness, alkalinity, and acidity determinations were 44.3 (42–48), 42.6 (38–45), and 4.1 (1–12) mg/liter as $CaCO_3$, respectively. The pH ranged from 6.8 to 7.6, and the mean and range for dissolved oxygen was 8.5 (4.0–11.9) mg/liter. All water characteristics were measured by methods described by the APHA et al. (1971).

Toxicant solution — Lead nitrate [anhydrous, $Pb(NO_3)_2$, reagent grade] was dissolved in distilled water and introduced to the diluter by a chemical-metering device (Mount and Warner 1965). Lead concentrations (Table 1) were assigned by stratified random assignment to each test tank.

Water samples (25 ml/day) were taken Monday through Friday from each adult spawning tank and larval growth tank with fish present. These water samples were acidified to pH 2.5–3.0 and composited for 2-wk periods. All duplicate tanks were analyzed for lead every 2 wk, providing 60 analyses at each duplicate concentration.

Lead analyses before July 1973 were performed by extraction of the ammonium pyrollidine dithiocarbamate (APDC)-lead complex into methyl isobutyl ketone (MIBK) and subsequent analysis by atomic absorption spectrophotometry (AAS) (Brooks et al. 1967) Calibration curves constructed by the method of known additions of lead to control water were used in the analyses. Differentiation between

TABLE 1. Survival, spawning, and egg production of first- and second-generation brook trout (*Salvelinus fontinalis*) exposed to various concentrations of lead.

	Total lead (μg/liter)											
	472.4[a]	474.8	235.0	235.4	118.6	119.8	57.9	57.3	34.1	32.8	0.9 (Control)	0.8 (Control)
	±14.2	±16.8	±6.5	±7.1	±4.2	±4.0	±2.1	±2.2	±1.4	±1.4	±0.2	±0.2
	A[b]	B	A	B	A	B	A	B	A	B	A	B
First generation												
Adult survival during spawning (%) (Oct. 1971–Jan. 1972)	100	60	80[c]	80[c]	100	80[c]	100	100	100	100	60[c]	80[c]
No. mature ♂	2	2	2	2	2	2	1	1	2	2	3	2
No. mature ♀	3	3	3	3	3	3	4	2	3	3	2	3
No. ♀ spawning	2.0	0	1.0	3.0	3.0	2.5	4.0	0[d]	2.5	3.0	1.5	2.5
Mean spawnings/♀	2.0	—	3.0	2.7	2.7	2.4	1.8	0	2.0	3.3	3.3	4.0
Mean viable eggs spawned/♀	367	—	562	548	638	323	350	—	383	611	551	462
Second generation												
Adult survival during spawning (Sept. 1973–Feb. 1974)	0[e]	—	—[f]	—[f]	50[d]	100	100	67[d]	100	100	100	83[d]
No. mature ♂	—	—	—	—	1	2	2	2[g]	2	2	2	2
No. mature ♀	—	—	—	—	5	4	4	3[g]	4	4	4	4
No. ♀ spawning	—	—	—	—	1.5	3.0	2.5	2.0	3.5	4	2.0	2.5
Mean spawnings/♀	—	—	—	—	3.3	1.7	1.6	3.0	3.1	3.0	6	3.2
Mean viable eggs spawned/♀	—	—	—	—	0	411	163	236	264	650	187	403

[a]Mean and 95% confidence interval; [b]A and B represent duplicate adult spawning tanks; [c]Deaths due to fighting; [d]Disease-related deaths; [e]All fish died before reaching sexual maturity; [f]Fish were physically unable to spawn because of severe scoliosis and were therefore terminated before spawning; [g]No successful reproduction occurred in first-generation trout; therefore second-generation spawners from A were divided equally between duplicates at time of spawning.

lead that would pass through a 0.10-μm pore size membrane filter (dissolved lead approximation) and lead present without filtering the samples (total lead approximation) was made by using the APDC–MIBK and AAS method on 14 unacidified "grab" samples from each chronic concentration and from two samples from an acute concentration of 4760 μg total Pb/liter. Mean percentages of dissolved lead and 95% confidence intervals for mean total chronic lead concentrations of 34, 58, 119, 235, and 474 μg/liter were 62 ± 7.1, 68 ± 9.2, 71 ± 7.5, 75 ± 7.3, and 81 ± 6.9, respectively. Mean percentage of dissolved lead for acute samples was 82.

After July 1973 anodic stripping voltammetry (ASV) on acid digested samples (J. Poldoski, Environmental Research Laboratory–Duluth, Duluth, Minn., personal communication) and furnace AAS were used to analyze bioassay water samples. Comparisons between extraction–AAS and these latter two methods for lead analysis showed that the latter methods were faster, more sensitive, and agreed well in accuracy with the extraction method. The accuracy of the furnace AAS method was verified by analyzing reference water samples obtained from the Environmental Protection Agency's Analytical Quality Control Laboratory in Cincinnati, Ohio. Three samples specified to be 28, 92, and 350 μg Pb/liter were found to be 28, 88, and 295μg Pb/liter, respectively, using this method. The furnace AAS method and the ASV method were compared by analyzing eight sets of samples from all concentrations and agreement between these methods was found to be within ± 4% for all lead concentrations.

BIOLOGICAL

This study involved 1) exposure of yearling brook trout through spawning (May 1971–January 1972); 2) exposure of the offspring from the initial parental group through spawning (November 1971–February 1974); and 3) exposure of offspring from the second parental group to the juvenile stage (November 1973–May 1974) (Fig. 1). Biological methods for these three generations will be given separately.

First generation — Yearling through adult spawning — Yearling brook trout (50–70 g) were obtained from the Cedar Island Hatchery in Brule, Wisconsin. Fish were acclimated to laboratory conditions for 4 wk before starting the exposure. The experiment began in May 1971 when 32 fish per duplicate were placed by stratified random assignment in each of the 12 exposure tanks. Sex was determined on all fish in September 1971, and they were separated into groups of males and females. Fish were then thinned randomly to a sex ratio of two males to three females, and one spawning substrate was placed in each adult spawning tank. Spawning commenced in November 1971 and continued until mid-December. Experimental procedures used during spawning and parental termination were the same as those described by McKim and Benoit (1971).

After exposures of 2, 9, 20, and 38 wk, subsamples of 4–10 fish per duplicate were anesthetized with M.S.222 (ethyl *m*-aminobenzoate methanesulphonate). Blood was then drawn with a heparinized syringe by caudal puncture, and gill, liver, kidney, gonad, spleen, and muscle samples were dissected. All tissues were rinsed with distilled water, individually wrapped in cellophane, and frozen along with blood samples for subsequent lead analysis (Leonard 1971). Mean percentage recovery and 95% confidence interval of 34 tissue samples spiked at 20 and 40 μg Pb/liter was 107 ± 11.4%.

Second generation — Embryo through adult spawning — Exposure of the second-generation brook trout through one complete life cycle began with the spawning of the first-generation fish (Fig. 1). Bio-

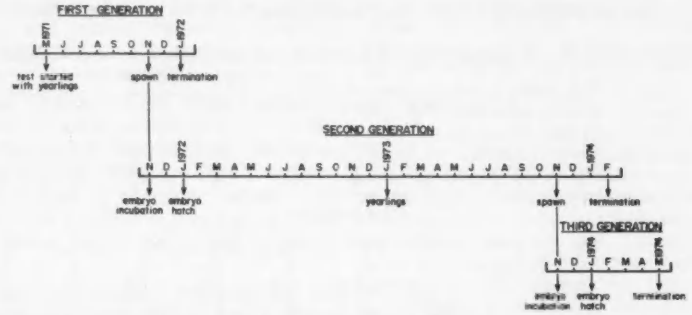

FIG. 1. Chronological order of exposure of three generations of brook trout (*Salvelinus fontinalis*) to lead.

logical methods used during embryo incubation and alevin–juvenile survival and growth studies were the same as those described by McKim and Benoit (1974). Weights were determined on all alevins at hatch and on a subsample of 40 juvenile fish per concentration, 16 wk after hatching. Juveniles were transferred from the larval growth chambers to the adult spawning tanks 12 wk after hatching. All fish were separated according to sex in September 1973 and randomly thinned to a sex ratio of two males to four females in all tanks. Two artificial spawning substrates (Benoit 1974) were placed in each tank, and spawning commenced in November 1973. Experimental methods used during spawning and parental termination were the same as those used for first-generation fish.

Two to five fish from each duplicate tank were randomly selected and anesthetized with M.S. 222 at 46, 70, and 105 wk after hatch. Tissues, including brain, were sampled and frozen for lead analysis as previously described for first-generation fish. Remaining fish in each concentration after 105 wk of exposure were finclipped for identification and transferred to control water. After 12 wk in control water, two fish from each former lead concentration and controls were anesthetized, and gill, liver, and kidney tissues were dissected and analyzed for lead. These tissue samples were used to determine the dissipation of accumulated lead.

Third generation — Embryo through 12-wk-old juveniles — The third-generation exposure began with spawning of the second-generation fish (Fig. 1). This generation was exposed throughout the embryo stage and for 12 wk following hatch. Biological methods were the same as those given for the second-generation alevins except that weights were determined on all surviving juvenile fish 12 wk after hatching.

Ten eggs per duplicate at spawning and two to four alevins per duplicate at hatch and at 1, 2, 4, 8, and 12 wk after hatch were sampled and preserved in 4% formaldehyde solution for lead-residue analysis. Lead residues from alevins preserved in formaldehyde were compared with alevins preserved by freezing at all exposure concentrations and no detectable differences were found between the two methods of preservation.

Trout diets and treatment of diseases and ectoparasites — All fish were fed measured amounts of a commercial trout food (Oregon Moist[1], Glencoe Mills[2], Silver Cup[3], and Ewos[4])[5,6] daily. Food rations were calculated bimonthly by multiplying the total body weight of each individual group of exposed fish by a percentage of body weight ranging from 0.7 to 3.4% depending on the average weight of the fish and water temperature.

Diseases and ectoparasites were treated with neomycin, tetracycline, and formaldehyde as described by The Committee on Methods for Toxicity Tests with Aquatic Organisms (1975). Secondary fungal growth (*Saprolegnia*) was controlled by swabbing with a 1% solution of malachite green.

Statistics — Growth and spawning data were subjected to a one-way analysis of variance with an *F*-test of significance ($P \geqslant 0.05$) and subsequent analysis with the Student's *t*-test ($P \geqslant 0.05$) (Steel and Torrie 1960).

Acute toxicity test — A 96-h acute toxicity test was conducted at 12 ± 1 C with 72-wk-old unexposed brook trout (102 g) from the same group used to begin the chronic test. This continuous-flow test with 10 fish per duplicate was conducted according to methods described by The Committee on Methods for Toxicity Tests with Aquatic Organisms (1975).

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[1]Bioproducts, Inc., Warrenton, Oregon 97146

[2]Glencoe Mills, Inc., Glencoe, Minn. 55336, USA.

[3]Murray Elevators, Murray, Utah 84107, USA.

[4]Astra Pharmaceutical Co., Worcester, Massachusetts 01606.

[5]Selection of these commercial diets was based on pesticide content and availability.

[6]Samples from all diets were analyzed for lead and were found to be within the range of 3.6–6.5 μg Pb/g (dry wt).

Results

First Generation

During the 38-wk exposure of brook trout no effects caused by lead on growth, survival, or spawning behavior were observed (Table 1). Means and 95% confidence interval of the lengths and weights of all test fish at thinning were 24.4 ± 1.3 cm and 175.2 ± 27.2 g, respectively. No spawning occurred in one duplicate tank at mean exposure concentrations of 58 and 474 μg Pb/liter; however, spawning did occur in the other duplicates at these concentrations. Mean viable eggs spawned per female at all lead concentrations tested was not significantly different ($P \geq 0.05$) from the controls.

Several yearling trout became hyperactive after 3-wk exposure to 474 μg Pb/liter and would often swim erratically, lose equilibrium, and/or experience muscular spasms when disturbed. Severity of the muscular spasms at this concentration tended to increase with increasing exposure time.

Residue values from the gill, liver, kidney, muscle, spleen, gonads, and red blood cells sampled throughout the 38-wk exposure of trout to 235 μg Pb/liter showed that the kidney accumulated the greatest amount of lead and the gill and liver the next greatest amounts (Fig. 2). Residues from the gill, liver, and kidney tissues of fish from all exposure concentrations were greater than from control tissue. They appeared to reach equilibrium on a micrograms-lead-per-gram basis after 20-wk exposure to 474 and 235 μg Pb/liter, but did not reach equilibrium at lower exposure concentrations (Fig. 3). Spleen and gonads of fish exposed to 235 μg Pb/liter accumulated small amounts of lead (Fig. 2). Muscle tissues from fish exposed to all concentrations accumulated small amounts of lead; however, these levels were not related to exposure concentrations. Red blood cells accumulated lead in direct proportion to increasing concentrations during the first 9 wk of exposure. After 20 wk exposure, residues in the red blood cells from fish exposed to 119, 235, and 474 μg Pb/liter had decreased, and then began to increase and apparently had not reached equilibrium after 38 wk of exposure. On the other hand, red blood cells from fish exposed to 34 and 58 μg Pb/liter appeared to reach equilibrium on a micrograms-per-gram basis after 2 wk (Fig. 3).

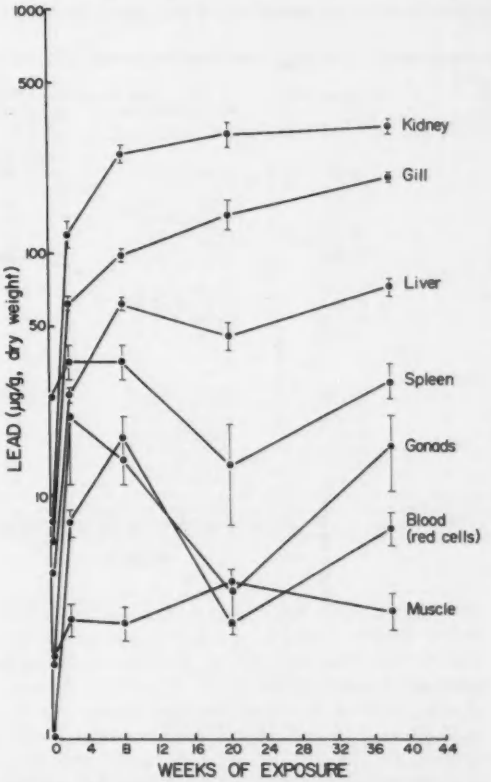

FIG. 2. Lead residues (micrograms per gram dry weight) from various tissues of first-generation brook trout exposed to 235 μg Pb/liter. (●), represents the mean and SE of 10 samples.

Second Generation

Percentages of alevins at hatch with spinal deformities (scoliosis) were 58, 21, 5, 9, 6, and 1, respectively, at concentrations of 474, 235, 119, 58, 34, and 0.9 μg Pb/liter (control). Each alevin hatching with scoliosis was counted as an unsuccessful hatch and discarded. Therefore, because of the large number of spinal deformities, mean hatchability of embryos exposed to 474 and 235 μg Pb/liter was reduced to 28 and 64%, respectively (Table 2). Alevin–juvenile survival and growth after 16-wk exposure to 474 μg Pb/liter were significantly reduced ($P \geq 0.05$) (Table 2). Growth of 65-wk-old fish exposed to 235 μg Pb/liter was also reduced; however, these severely deformed fish were terminated before final growth measurements were taken. There were no effects on growth or survival of fish throughout the entire exposure period at 119 μg Pb/liter and below. Means and 95% confidence interval of lengths and weights of these fish at thinning were 28.5 ± 3.7 cm and 312 ± 66 g, respectively.

Estimated number of eggs per female was multi-

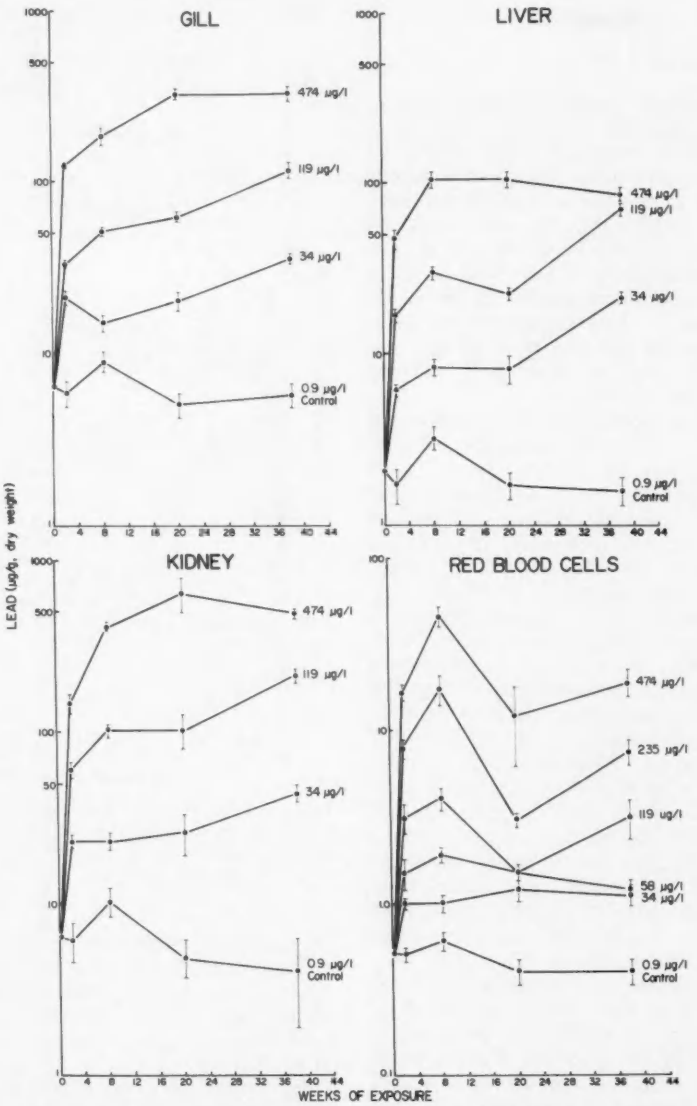

FIG. 3. Lead residues (micrograms per gram dry weight) from gill, liver, kidney, and red blood cells of first-generation brook trout exposed to various concentrations of lead. (●), represents the mean and SE of 10 samples.

plied in succession by percent hatchability, percent alevin–juvenile survival, and individual juvenile weights to yield an estimated total weight of 16-wk-old young per female at each exposure concentration. Combined reduction in hatchability, survival, and growth at 474 μg Pb/liter caused the estimated total weight of 16-wk-old fish produced per female to be significantly lower ($P \geqslant 0.05$) (Table 2). Estimated total weight of 16-wk-old young per female from all lead concentrations was divided by estimated total weight of 16-wk-old young per female in the controls

TABLE 2. Estimated total weight of second- (16-wk-old) and third- (12-wk-old) generation brook trout produced per female at various lead concentrations.

Mean total Pb concn (μg/liter)	Duplicates	Estimated[a] eggs/female	×	Hatchability (%)	×	Alevin–juvenile survival (%)[b]	×	Individual juvenile wt (g)	=	Estimated total wt of young/ female (g)	Ratio estimated total wt young/female (exposed: control)
						Second generation					
474	A	262		28(4)[d]		20		2.1[e] ± 0.18[f](7)[g]		30.8	0.03
	B	—[c]		—		—		—		—	
235	A	401		73(3)		92		3.4 ± 0.08(20)		915.66	0.81
	B	391		60(8)		96		3.4 ± 0.38(20)		765.73	
119	A	456		86(7)		100		3.1 ± 0.16(20)		1,215.69	0.84
	B	231		85(6)		98		2.7 ± 0.50(20)		519.54	
58	A	250		79(7)		90		3.8 ± 0.33(20)		675.45	0.65
	B	—[h]		—		—		—		—	
34	A	274		57(5)		90		2.8 ± 0.06(20)		393.57	0.75
	B	436		95(9)		82		3.4 ± 0.05(20)		1,154.79	
0.9 (Control)	A	394		100(5)		84		3.6 ± 0.44(20)		1,191.46	1.00
	B	330		96(6)		66		4.2 ± 0.11(20)		878.17	
						Third generation					
119	A	—[i]		—		—				—	0.43
	B	270		70(4)		96		0.88[e] ± 0.07(41)		159.67	
58	A	106		96(2)		98		1.33 ± 0.09(44)		132.63	0.83
	B	155		81(3)		94		1.47 ± 0.05(40)		173.49	
34	A	173		86(3)		92		1.16 ± 0.11(42)		158.78	1.56
	B	427		94(6)		90		1.18 ± 0.10(40)		419.04	
0.9 (Control)	A	123		86(1)		94		1.27 ± 0.09(44)		126.28	1.00
	B	265		84(4)		94		1.17 ± 0.15(15)		244.82	

[a]Number of viable eggs produced per spawning female × the probability of spawning (i.e. total spawners/total females = 0.7143 for second and 0.6562 for third generation); [b]Fifty fish exposed in each duplicate; [c]No viable eggs produced; [d]Number of spawnings checked for hatchability; [e]Significantly less than controls ($P = 0.05$, analysis of variance with t-test); [f]Mean and 95% confidence interval; [g]Number of fish sampled; [h]Disease problem; [i]Parental fish suffered moderate scoliosis; therefore, no viable eggs were produced.

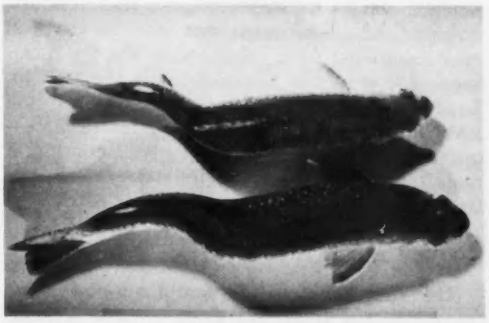

FIG. 4. Deformed 65-wk-old second-generation brook trout exposed to 119 μg Pb/liter.

to yield a ratio which was used to compare estimated total weight produced at each lead concentration to the controls (Table 2). This ratio was lower than the control ratio at all exposure concentrations, but the only marked decrease below 50% of the control ratio was at 474 μg Pb/liter.

Hyperactivity, similar to that observed in first-generation brook trout exposed to 474 μg Pb/liter, was first noted in the offspring 8 wk after hatch at this concentration. When disturbed, these juveniles swam erratically and often underwent muscular spasms that appeared to leave them paralyzed for several minutes.

Scoliosis developed in 33% of the alevins that appeared normal at hatch and 39% of all juveniles exposed to 474 μg Pb/liter before 100% mortality occurred at this concentration in December 1972 after 46 wk of exposure. Blackening of the caudal peduncle area of several juvenile brook trout exposed to 235 and 119 μg Pb/liter was first observed after 15 and 27 wk, respectively. All trout with black tails exposed to these concentrations gradually developed scoliosis, which continued to become more severe with longer exposure time. After 65 wk of exposure to 235 and 119 μg Pb/liter, the percentages of fish with scoliosis were 100 and 34, respectively (Fig. 4). Scoliosis was so severe at 235 μg Pb/liter that all fish were physically unable to spawn and were therefore terminated 65 wk after hatch. Fish exposed to 58 μg Pb/liter and below were not affected with blacktail or scoliosis throughout the exposure period.

Spawning occurred at mean lead concentrations of 119, 58, and 34 μg/liter and in the control, and the number of viable eggs produced per female was not significantly different ($P \geq 0.05$) between exposures and control (Table 1). However, no viable eggs were produced in one duplicate tank at 119 μg Pb/liter, because three out of the four females in this duplicate suffered from moderate scoliosis which severely limited their spawning mobility and agility.

Lead-residue uptake and accumulation trends in gill, liver, kidney, muscle, spleen, and gonad tissues of trout were quite similar to residues de-

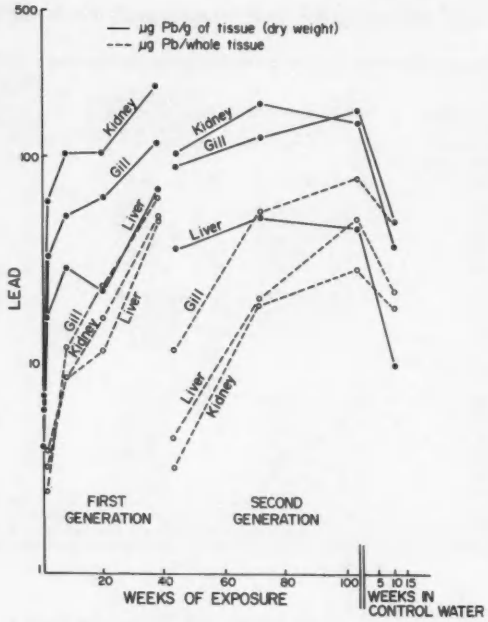

FIG. 5. Lead residues from tissues of first- and second-generation brook trout exposed to 119 µg Pb/liter, and dissipation of residues from tissues of second-generation trout placed in control water. (●), represents the mean of 10 samples.

scribed earlier for first-generation trout. Lead residues (micrograms) per gram of tissue (dry weight) and the lead residue in total tissue from the gill, liver, and kidney of first- and second-generation brook trout exposed to 119 µg Pb/liter are shown in Fig. 5. Total lead present in the gill, liver, and kidney of second-generation fish continued to increase as the fish increased in size. Lead residues per gram of tissue in liver and kidney samples tended to level off and apparently reach an equilibrium but, lead residues per gram of gill tissue continued to increase throughout the exposure and no equilibrium level was achieved. Mean average lead residue values for all muscle tissue sampled from second-generation fish exposed to 119 µg/liter and from control fish were 2.1 and 1.1 µg Pb/g, respectively. Brain tissues did not appear to accumulate lead residues at any exposure concentration.

Gill, liver, and kidney tissues dissected from trout that were exposed to 119 µg Pb/liter for 105 wk and then placed in control water for 12 wk showed a reduction of 70%, 78%, and 74%, respectively, in micrograms of lead per gram of tissue (Fig. 5). Total amount of lead in these tissues was reduced by 39%, 56%, and 35%, respectively (Fig. 5).

THIRD GENERATION

Exposure to 119 µg Pb/liter reduced the hatchability of embryos (Table 2). This reduction was due to the large number of alevins with scoliosis, each of which was counted as an unsuccessful hatch and discarded. Percentage of alevins hatching with scoliosis at 119 µg Pb/liter was 21, whereas 2% hatched with scoliosis at 58 and 34 µg Pb/liter and in the control. Juvenile weights at 12 wk were significantly lower ($P \geqslant 0.05$) at 119 µg Pb/liter (Table 2). Survival after 12 wk exposure was not affected by lead. The ratio of estimated total weight of fish produced per female was 57% lower than the control ratio at 119 µg Pb/liter and was 56% higher than the control ratio for fish exposed to 34 µg Pb/liter (Table 2).

Subsamples of eggs at spawning and alevins 4 wk after hatch showed that lead residues increased with higher exposure concentrations (Table 3). Embryos contained more lead at each higher exposure concentration. Samples of newly hatched alevins showed negligible lead residues, however, which indicated that most of the lead residues present were contained in the egg membrane and were not accumulated in the embryo. Lead residues in third-generation alevins and juveniles accumulated steadily with increasing exposure time and with increasing lead concentrations throughout the 8 wk following hatch and then appeared to decrease 12 wk after hatch.

ACUTE TOXICITY

The 96-h LC50 of the continuous-flow acute test conducted at 12 ± 1 C on 72-wk-old brook trout was calculated by graphical extrapolation on semilogarithmic paper to be 4100 µg Pb/liter (based on total lead).

MATC AND APPLICATION FACTORS

Effects of lead on survival, growth, and reproduction of brook trout in water with a hardness of 44 mg/liter (as $CaCO_3$) and a pH of 6.8–7.6 demonstrated that the maximum acceptable toxicant concentration (MATC) for this species lies between 58 and 119 µg Pb/liter (based on total lead). The application factor (MATC/96-h LC50) based on total lead lies between 0.014 and 0.029. The MATC and 96-h LC50 values determined using total lead measurements were multiplied by the percentage of filterable lead found to be present at these lead concentrations to obtain a dissolved lead approximation. This multiplication

TABLE 3. Lead residues (micrograms per gram) of third-generation eggs and alevin-juveniles exposed to various water concentrations of lead.

Mean total Pb concn in water (μg/liter)	Eggs at spawn	Wk alevin–juvenile exposed to Pb						
		Hatch 0	1	2	3	4	8	12
119	2.01[a]	0.16 (0.0151)[b]	3.6 (0.0139)	9.6 (0.0124)	9.4 (0.0116)	33.2 (0.0098)	43.8 (0.0427)	20.1 (0.2227)
58	1.70	0.16 (0.0160)	0.16 (0.0159)	0.18 (0.0146)	3.7 (0.0131)	20.1 (0.0121)	25.3 (0.0605)	12.7 (0.2375)
34	0.89	0.18 (0.0143)	0.19 (0.0138)	0.25 (0.0123)	3.40 (0.0113)	10.0 (0.0111)	11.7 (0.0610)	8.0 (0.1776)
0.9 (Control)	0.25	0.19 (0.0136)	0.20 (0.0129)	1.29 (0.0121)	0.24 (0.0112)	0.25 (0.0100)	0.06 (0.0348)	0.36 (0.2287)

[a]Each value represents an average of 20 eggs analyzed.
[b]Mean dry weight in grams of three fish analyzed.

yielded an MATC between 39 and 84 μg/liter based on dissolved lead and a 96-h LC50 of 3362 μg/liter for dissolved lead. The application factor based on dissolved lead lies between 0.012 and 0.025.

Discussion

Results of this study indicated that concentrations of 119 μg Pb/liter and above have an adverse effect on brook trout exposed through several successive generations. The embryo, alevin, and early juvenile life stages of brook trout apparently are more sensitive to lead than later stages in the life cycle. Blackened caudal peduncles, which occurred in second-generation juveniles after 15–27-wk exposure to 119 μg Pb/liter and higher, always preceded the development of scoliosis. In some cases the blacktail condition disappeared after severe scoliosis had developed. Davies and Everhart (1973) also found the alevin and juvenile life stages of rainbow trout to be more sensitive to lead than adults and reported similar occurrences of blacktail and scoliosis in juvenile fish. Haider (1964) produced a blackened caudal region in rainbow trout by injecting lead into the top of the pelvic fins. He also found that trout given lead in their daily food became darkened. The present study showed that spinal curvatures observed in brook trout, which were generally bent toward the left, originated in the region just posterior to the dorsal fin in the same area associated with the blacktail condition (Fig. 4). When brook trout which had recently developed scoliosis were anesthetized in M.S. 222 during periods of blood and tissue sampling, their muscles relaxed and the fish straightened out. Spinal curvatures returned, however, when they were revived. This response indicated that lead was affecting the muscles of the caudal region. Fish that had scoliosis for several weeks did not straighten out under anesthesia, indicating that their spines had possibly become calcified in this deformed position. A biochemical inhibition of metabolism could be responsible for the blacktail and spinal curvature symptoms in brook trout. Nutritional deficiencies of the amino acid tryptophan and the vitamin ascorbic acid have also been found to cause scoliosis and lordosis in trout (National Academy of Sciences 1973). Fati (1961) suggested that lead interferes with the enzymatic degradation of tryptophan, and Pakkala et al. (1972) stated that lead could be a possible enzyme inhibitor because of its affinity for amino, imino, and sulfhydryl groups which comprise reactive sites on enzymes.

Hyperactivity, erratic swimming, muscular spasms, and loss of equilibrium noted in brook trout exposed to 474 μg/liter of lead suggested that lead was affecting the nervous systems of these fish. Haider (1964) obtained similar symptoms of erratic swimming, wave-type muscular movements, and loss of equilibrium in rainbow trout exposed to lead. Previous work has also shown that lead affects the nervous systems of human beings and frogs (Chisholm 1971; Manalis and Cooper 1973).

Since lead residues in liver and kidney apparently reached an equilibrium, analysis of these tisues might be useful in predicting whether or not wild trout populations are being chronically subjected to sublethal lead concentrations that could cause potential damage to the population. Maximum mean residue concentrations for liver and kidney samples of first- and second-generation fish exposed to 119 μg Pb/liter were 68 and 50 μg Pb/g of liver tissue, and 215 and 179 μg Pb/g of kidney tissue, respectively. Lead residues in wild

trout approximating these concentrations in liver and kidney tissue could be detrimental and/or indicate detrimental exposures, since spinal deformities occurred in some laboratory trout with tissue residues of this magnitude and above. Lead residues in gill tissue did not reach an equilibrium according to the micrograms of lead present in a gram of tissue, but tended to increase with continuing exposure (Fig. 5). Similar results were obtained by Pagenkopf and Neuman (1974) with gill and liver tissue from brook trout exposed to 2.81 μg Pb/liter. They found that on a microgram-per-gram basis lead residues in gill tissue continued to increase with age of the fish, whereas liver residues were highest between 1 and 2 yr of age and appeared to reach equilibrium and remain fairly constant in the older fish. Muscle tissue sampled from fish in the present study did not appear to accumulate lead to any substantial degree. Pakkala et al. (1972) analyzed 419 beheaded and eviscerated fish of various species from 17 locations in New York State and also found lead residues to be quite low (range = 0.3–3.0 μg Pb/g) in these samples, which represent primarily muscle tissue. Gonad tissue from first-generation fish exposed to 235 and 474 μg Pb/liter and second-generation fish exposed to 119 μg Pb/liter in the present study had accumulated lead residues before spawning that were higher than control residue levels. After spawning, gonad tissues appeared to accumulate small quantities of lead, but the gonads at this time were in a state of atrophy and the decrease in tissue weight probably accounted for the apparent increase in residues.

Dissipation of lead from tissue of exposed brook trout that were transferred to control water for up to 12 wk indicated that lead was excreted to some degree. After 2 wk in control water, lead was apparently being relocated in the fish. Gill and kidney tissues were losing lead, while liver tissue was further accumulating lead. After 12 wk in control water, however, the gill, kidney, and liver tissues all contained significantly lower lead residues than initially.

The greatest increase in lead residues in third-generation alevins corresponded to the interval when yolk-sac absorption was complete and alevins began to feed (Table 3). Alevins were losing weight and beginning to use their gills during yolk-sac absorption. Rapid uptake of lead through the gills combined with loss of weight probably accounts in part for the high microgram-per-gram lead residue values 4 wk after hatch. Total microgram uptake of lead continued to increase in juveniles at 12-wk exposure, but the microgram-per-gram uptake of lead appears to have decreased. This was probably caused by the rapid growth during this period.

The application factors for lead-exposed brook trout in Lake Superior's soft water lies between 0.014 and 0.029 for total lead and 0.012 and 0.025 for dissolved lead. The application factor calculated using total lead is close to the application factor calculated using dissolved lead. Goettl et al. (1974) obtained an application factor for rainbow trout exposed to lead in hard water of 0.0002–0.0008 when total lead present was used in the calculations, but an application factor of 0.01–0.02 when concentrations of dissolved lead were used. They also calculated an application factor based on the total lead present of 0.006–0.012 with rainbow trout exposed to lead in soft water (28 mg/liter $CaCO_3$). Considering inherent biological variation between groups of fish, the agreement between the application factors calculated for this study and the application factors calculated for rainbow trout exposed to lead in hard and soft water are good, if the hard water application factor calculated on dissolved lead is used.

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Phosphorus Retention Capacity of Lakes

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LARSEN, D. P., and H. T. MERCIER. 1976. Phosphorus retention capacity of lakes. J. Fish. Res. Board Can. 33: 1742–1750.

Mean annual lake phosphorus concentrations ($[P]_x$) in a steady state system can be described as a function of two variables, the mean annual influent P concentration and the net annual P sedimentation: $[P]_x = [\bar{p}]\ (1 - R_p)$ (see Rigler 1975). $[\bar{p}]$ is the annual P supply/annual water supply and R_p is that fraction of inflowing P retained by the sediments annually. Since R_p is critical in determining $[P]_x$, lake properties were examined for their influence on R_p; the best fit empirical expressions developed related R_p to either areal water supply (annual water inflow rate/lake surface area) or hydraulic washout coefficient (annual water outflow rate/lake volume). The expressions were derived from characteristics of low productivity lakes; their validity for more productive lakes was not examined.

A graph of $[\bar{p}]$ vs. R_p is proposed to illustrate the relationship between $[P]_x$, $[\bar{p}]$, and R_p, and, if lake P concentrations are used as measures of trophic state, this graph is useful for predicting trophic state and changes in trophic state caused by altering $[\bar{p}]$ and/or R_p. It is conceptually similar to those of Vollenweider (1975) and Dillon (1975) but differs in that it separates the potential lake concentration ($[P]_x$ would be equal to $[\bar{p}]$ if P were conservative) from those factors acting to reduce $[\bar{p}]$, expressed as R_p, to produce lake concentrations.

LARSEN, D. P., and H. T. MERCIER. 1976. Phosphorus retention capacity of lakes. J. Fish. Res. Board Can. 33: 1742–1750.

Les concentrations moyennes annuelles de phosphore dans un lac ($[P]_x$) dans un système en état d'équilibre peuvent être décrites comme étant fonction de deux variables, la concentration moyenne annuelle du P d'entrée et la sédimentation annuelle nette du P : $[P]_x = [\bar{p}]\ (1 - R_p)$ (voir Rigler, 1975). $[\bar{p}]$ est le quotient apport annuel de P/apport annuel d'eau et R_p est cette fraction du P d'entrée qui est retenue par le sédiment en un an. Etant donné que R_p joue un rôle critique dans la détermination de $[P]_x$, nous avons étudié les propriétés du lac en vue de déterminer leur influence sur R_p; d'après les meilleures exressions développées empiriquement, R_p est fonction soit des apports d'eau par superficie (taux annuel d'entrée d'eau/superficie de la surface du lac) soit du coefficient de lavage hydraulique (taux annuel de sortie d'eau/volume du lac). Nous avons établi ces formules à partir des caractéristiques de lacs peu productifs; nous n'avons pas vérifié leur validité pour des lacs plus productifs.

Nous proposons un graphique de $[\bar{p}]$ vs. R_p pour illustrer la relation entre $[P]_x$, $[\bar{p}]$, et R_p. Si les concentrations de P dans le lac sont utilisées comme mesures de l'état trophique, ce graphique permet également de prédire l'état trophique et les changements qu'entraîne dans l'état trophique une altération de $[\bar{p}]$ et/ou de R_p. Dans son concept, le graphique est semblable à ceux de Vollenweider (1975) et de Dillon (1975). Il en diffère cependant en ceci qu'il sépare la concentration potentielle dans le lac ($[P]_x$ serait égale à $[\bar{p}]$ si P était faible) des autres facteurs causant une diminution de $[\bar{p}]$, exprimé sous forme de R_p, pour produire les concentrations dans le lac.

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MASS balance models have been developed to describe the relationship between phosphorus (P) concentrations in lakes and the supply of P to lakes (see review by Dillon 1974; Imboden 1973, 1974; Lerman 1974; Lorenzen 1973; Snodgrass and O'Melia 1975; Sonzogni et al. 1974; Vollenweider 1969, 1975). Because lake P concentrations can be used as an indication of trophic state (Sawyer 1947; Vollenweider 1968; Dillon 1975), these models can be useful for predicting water quality and changes in water quality associated

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with changes in P supply. In the simplest form, these models state that on an annual basis the change in P content of lakes is related to P inflow, outflow, and sedimentation:

$$\frac{dP}{dt} = J - Q \cdot [P] - S \qquad (1)$$

where [P] is the mean P concentration in the lake; J, the rate of external P supply; Q, the water outflow rate; and S, the net P sedimentation rate. The steady state solution to equation (1) is:

$$[P]_\infty = \frac{J - S}{Q} \qquad (2)$$

Assumptions underlying equation (1) are: rate of water inflow and outflow are steady and equal; the system is well mixed at all times; and a net loss of P to the sediments occurs on an annual basis.

The net fraction of inflowing P deposited on the sediments is S/J and has been defined by Vollenweider (1975) in a slightly different way as the P retention coefficient, R_p. Thus, substituting $J \cdot R_p$ for S, equation (2) can be written:

$$[P]_\infty = [\bar{p}]\ (1 - R_p) \qquad (3)$$

where $[\bar{p}] = J/Q$, the average influent P concentration (see Riger 1975). These equations describe the continuity of mass for P independent of the mechanisms by which the sedimentation term is described.

Equation (3) demonstrates the dependence of mean lake P concentrations on two variables, the mean influent P concentration, and the P assimilative capacity of lakes. We constructed a graph of $[\bar{p}]$ vs. R_p to show this relationship using data available from Dillon and Rigler (1974), Dillon (1975), and J. Gakstatter (Corvallis Environmental Research Laboratory, Corvallis, Oreg., 1974, personal communication): Although lakes generally violate some or all of the assumptions underlying the basic model, their trophic states agree well with those predicted from this relationship. This graph is similar in concept to those of Vollenweider (1975) and Dillon (1975). It is useful for predicting trophic state and changes in trophic state caused by manipulating influent P concentrations and/or manipulating a lake's P assimilative capacity.

The importance of the P retention capacity as a determinant of steady state lake concentrations is evident from equation (3). An examination of factors that control its magnitude is thus valuable for theoretical as well as practical purposes. Kirchner and Dillon (1975) and Chapra (1975) showed that the retention capacity could be related to areal water loading (q_s, annual water inflow rate/lake surface area). We present several other expressions that provide good statistical correlations between observed and predicted values of P retention capacity in lakes of low productivity. These relate the P retention capacity to either areal water loading or to the hydraulic washout coefficient ($\rho_w = Q/V$; V = lake volume).

Data Base

Three sources were used to obtain data to plot the position of lakes on a $[\bar{p}]$ vs. R_p graph and to determine relationships between R_p and lake properties. Dillon and Rigler (1974) and Dillon (1975) included estimates of L_p (areal P loading, g P/m^2 per yr), ρ_w (yr^{-1}), $\bar{z}$ (mean depth, meters) and R_{exp} for various lakes in North America and Europe. The quotient, $L_p/(\rho_w \cdot \bar{z})$ is assumed equivalent to $[\bar{p}]$ and $\rho_w \cdot \bar{z}$ equivalent to q_s because differences between water outflow and inflow rates are probably small. Vollenweider (1975) defined R_p as $\frac{\sigma_p}{\sigma_p + \rho_w}$ where σ_p (yr^{-1}) was the P deposition coefficient he hypothesized to describe P sedimentation as a function of the amount of P present in the lake as: $d[P]/dt = J/V - (\rho_w + \sigma_p)[P]$. Because a direct determination of its value is difficult to obtain and has not been determined for many lakes, R_p has generally been calculated as: $R_{exp} = 1 - \frac{\text{outflow load}}{\text{inflow load}}$ (Dillon and Rigler 1974). The distinction between R_p (as a theoretical value or as estimated by sedimentation measurements) and R_{exp} (as experimentally estimated from P inflow and outflow) will be maintained here, although they are equal at steady state if model assumptions are met. J. Gakstatter (Corvallis Environmental Research Laboratory, Corvallis, Oreg., 1974, personal communication) provided another source of data that includes ρ_w and $\bar{z}$, as well as inflow and outflow P concentrations and loadings, for many lakes in northeastern and midwestern United States studied by the U.S. Environmental Protection Agency's National Eutrophication Survey. Tables 1 and 2 summarize the data used.

The trophic status of lakes listed in Tables 1 and 2 were classified as O (oligotrophic), M (mesotrophic), E (eutrophic) and HE (hypereutrophic). These classifications are qualitative, based upon the assessments of limnologists who have investigated these lakes. In some cases, the identity of trophic state was not available.

$[\bar{p}]$ vs. R_{exp} Graph

Figure 1 was constructed from the data in

TABLE 1. Summary of lakes and characteristics used in Fig. 1. Data for lakes 1–17 were obtained from Dillon (1975) and references therein and for lakes 18–37 from J. Gakstatter (personal communication 1974).

No.	Lake	Trophic state	$[\bar{p}]$ ($\mu g/liter$)	R_{exp}	No.	Lake	Trophic state	$[\bar{p}]$ ($\mu g/liter$)	R_{exp}
1	Baldeggersee	E	230	0.61	19	Bemidji, Minn.	E	35	0.36
2	Bodensee-Obersee	E	200	0.65	20	Blackduck, Minn.	E	135	0.55
3	Erie	M-E	150	0.84	21	Chemung, Mich.	E	105	0.63
4	Greifensee	E	170	0.62	22	Clearwater, Minn.	E	180	0.76
5	Hallwilersee	O	75	0.36	23	Cokato, Minn.	E	385	0.44
6	Kalamalka	E	610	0.90	24	Delavan, Wis.	E	410	0.55
7	Kegonsa	E	505	0.09	25	Fremont, Wis.	HE	550	0.47
8	Monona	E	330	0.71	26	Green, Minn.	M-E	55	0.67
9	Michigan	O-M	85	0.9	27	Jordan, Mich.	E	130	0.17
10	Norrviken (1961–62)	E	425	0.49	28	Le Homme Dieu, Minn.	E	135	0.78
11	Okanagan	O	305	0.95	29	Nagawicka, Wis.	E	205	0.57
12	Pfaffikersee	E	195	0.77	30	Nest, Minn.	E	90	0.56
13	Sebasticook	E	90	0.48	31	Sebasticook, Maine	E	60	0.29
14	Skaha	M-E	95	0.65	32	Shawano, Wis.	E	35	0.23
15	Waubesa	E	620	0	33	Swan, Wis.	E	140	0.18
16	Wood	E	2590	0.90	34	Townline, Wis.	E	255	0.52
17	227 (ELA)	E	325	0.89	35	Trout, Minn.	E	375	0.92
					36	Wagonga, Minn.	E	4300	0.57
18	Beaverdam (Dodge County, Wis.)	E	265	0.0	37	Wapogasset, Wis.	E	70	0.43

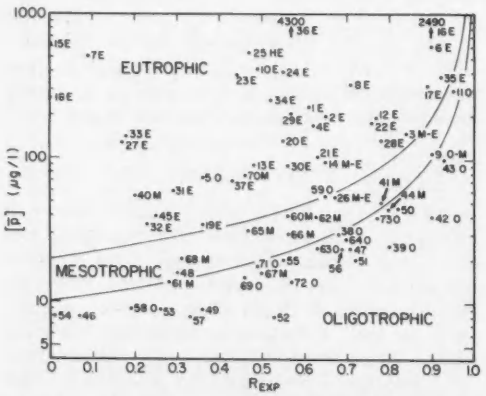

FIG. 1. Graph of mean tributary phosphorus concentration ($[\bar{p}]$) vs. phosphorus retention coefficient (R_{exp}) for lakes summarized in Tables 1 and 2. O = oligotrophic; M = mesotrophic; E = eutrophic; HE = hypereutrophic. Lines are solutions of equation (3) for $[\bar{p}]$ and R_{exp} values that produce lake concentrations of 10 and 20 μg/liter.

Tables 1 and 2, showing the modifying effect of a lake's P retention capacity upon the influent P concentration. Lines of constant lake P concentration can be drawn as solutions of Equation (3) for particular values of $[p]$ and R_p. If particular lake mean P concentrations can be used to designate the trophic state of a lake, curves delineating trophic states can be drawn, as adapted from Lerman (1974) and Dillon (1975). Dillon used lake concentrations of 10 and 20 μg/liter to separate oligotrophic (<10 μg/liter), mesotrophic (10–20 μg/liter) and eutrophic (>20 μg/liter) conditions. The same designations are used here.

The positions of the lakes on Fig. 1 agree reasonably with their trophic states. Some lakes violate the pattern. Several reasons can be suggested for their departure from the model and a more detailed investigation would be necessary to determine the cause of this discrepancy. Reasons for the discrepancies might be:

1) Observed lakes might not be in or near a steady state and, consequently, recent changes in $[\bar{p}]$ may not yet be reflected by changes in lake characteristics.

2) Data base for the calculations might be inadequate for the present analysis which requires an adequate estimate of the mean concentration of P in inflowing and outflowing waters. The optimum method for obtaining P flux into or out of lakes has only recently been critically evaluated (Treunert et al. 1974). Thus, the data reflect the notions of the principal investigators so sampling frequency may be neither consistent nor optimal.

3) Characteristics of some lakes may sufficiently disagree with model assumptions to invalidate a comparison. For example, vertical and horizontal inhomogeneities might be large enough

TABLE 2. Summary of lakes and characteristics used in Fig. 1 and for an analysis of relationships between R_{exp} and lake characteristics. Data for lakes 38–45 were obtained from Dillon (1975) and references therein, for lakes 46–57 from Dillon and Rigler (1974), and for lakes 58–73 from J. Gakstatter (personal communication 1974). Asterisks indicate lakes used for generating best empirical relationships between R_{exp} and lake characteristics.

No.	Lake	Trophic state	$[\bar{p}]$ ($\mu g/liter$)	R_{exp}	ρ_w (yr^{-1})	$\bar{z}$ (m)	σ_p (yr^{-1})
38	Aegerisee	O	30	0.68	0.115	49	0.24
39	*Clear	O	25	0.80	0.13	12.5	0.52
40	Leman	M	55	0.20	0.083	155	0.02
41	Ontario	M	50	0.78	0.152	84	0.54
42	*Superior	O	40	0.90	0.0053	148	0.05
43	*Tahoe	O	100	0.93	0.0014	303	0.02
44	Turlersee	M	45	0.80	0.465	14	1.86
45	Zurichsee	E	40	0.25	0.680	50	0.23
46	*Beech		8	0.07	22.7	9.8	1.71
47	*Bob		24	0.71	0.37	18.0	0.91
48	*Cameron		16	0.30	18.9	7.1	8.1
49	*Eagle-Moose		9	0.36	2.03	12.8	1.14
50	Four Mile		45	0.82	0.26	9.3	1.18
51	*Oblong-Haliburton		20	0.72	0.32	17.7	0.82
52	*Halls		8	0.53	0.96	27.2	1.08
53	*Maple		9	0.26	8.0	11.6	2.81
54	*Pine		8	0.01	18.5	7.4	0.19
55	Raven		20	0.55	14.9	0.73	18.2
56	Talbot		24	0.69	4.9	0.85	10.9
57	*Twelve Mile — Boshkung		8	0.33	2.38	18.1	1.18
58	*Bay of Naples, Maine	O	9	0.19	14.0	4.3	3.28
59	Canadaigua, New York	O	55	0.65	0.07	39.0	0.13
60	Carlos, Minn.	M	40	0.56	0.27	13.1	0.34
61	*Carry Falls, New York	O	14	0.28	9.61	5.4	3.74
62	Cass, Minn.	M	40	0.63	1.17	7.6	1.99
63	*Charlevoix, Mich.	O	24	0.63	0.31	16.8	0.53
64	Higgins, Mich.	O	28	0.70	.06	14.9	0.14
65	Houghton, Mich.	M	32	0.47	0.76	2.3	0.68
66	Long (Aroostook County, Maine)	M	30	0.56	0.31	13.4	0.39
67	*Long (Cumberland County, Maine)	M	16	0.50	0.83	10.4	0.83
68	*Mattawamkegg, Maine	M	20	0.31	8.69	3.7	3.90
69	*Moosehead, Maine	O	15	0.46	0.33	16.4	0.28
70	Pelican, Minn.	M	77	0.46	0.30	2.7	0.25
71	*Rangeley, Maine	O	18	0.49	0.36	14.3	0.35
72	*Sebago, Maine	O	14	0.57	0.19	30.8	0.25
73	Winnipesaukee, Minn.	O	40	0.77	0.25	13.1	0.84

to seriously affect the model assumption of a completely and instantly mixed system, or factors other than phosphorus might control trophic state.

4) Identity of trophic state is subjective so that designations are not likely to be universally acceptable.

Phosphorus Retention Capacity

Determining the P retention capacity is critical to the successful prediction of lake P concentrations. Empirically, R_p can be estimated from the ratio of outflow loads or concentrations to inflow loads or concentrations. Therefore, experimental determination of R_p is only as good as measurements of imported and exported P. Furthermore, steady state values are required if R_{exp} is to be representative of a particular lake. Here no attempts have been made to quantify the effect of deviation from steady state. Valid questions are: Can R_{exp} be related statistically to lake properties such as mean depth and hydraulic washout coefficient? Do these statistically derived relationships have theoretical foundation?

Kirchner and Dillon (1975) obtained a good

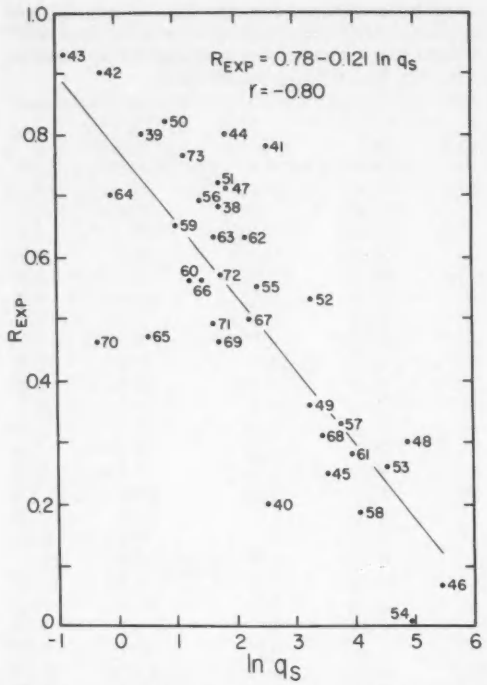

FIG. 2. Regression of R_{exp} on ln q_s for lakes summarized in Table 2.

relationship between R_{exp} and the areal water loading, q_s ($= \rho_{ic} \cdot z$; see Table 4), but did not obtain an expected good relationship between R_{exp} and the hydraulic washout coefficient.

Chapra (1975) and Dillon and Kirchner (1975) subsequently showed that a relationship of the form

$$R_{exp} = \frac{v}{v + q_s} \tag{4}$$

where v is an apparent settling velocity (meters per year) fit the data well. This expression can be derived from the definition of $R_p (= \sigma_p \cdot \bar{z} / [\sigma_p \cdot \bar{z} + \rho_{ic} \cdot \bar{z}] = v/[v + q_s]$, Dillon and Kirchner 1975).

Data summarized in Table 2 were analyzed to determine whether similar relationships existed, whether alternative relationships were equally valid, and particularly whether R_{exp} was related to ρ_w. Only lower mesotrophic or oligotrophic lakes were examined because increasing levels of productivity might decrease a lake's P retention capacity by providing an increasingly larger internal supply of P as anaerobic conditions develop (Vollenweider 1975) thus obscuring relationships between R_{exp} and other lake properties.

TABLE 3. Correlations between R_{exp} and various transformations and combinations of ρ_w and $\bar{z}$ for 20 lakes whose $[\bar{p}] \leq 25$ μg/liter (Table 2).

Correlation R_{exp} vs.	r	Correlation R_{exp} vs.	r
ρ_w	−0.74	$\frac{\bar{z}}{\rho_w}$	0.57
$\bar{z}$	0.33		
$\frac{1}{\rho_w}$	0.68	$\frac{\rho_w}{\bar{z}}$	0.00
$\frac{1}{\bar{z}}$	0.18		
ln ρ_w	−0.77	ln $\frac{\bar{z}}{\rho_w}$	0.58
ln $\bar{z}$	0.09	$\bar{z}^2$	0.34
$\rho_w \cdot \bar{z}$	−0.80	ρ^2_w	−0.69
ln $\rho_w \cdot \bar{z}$	−0.92	$\frac{1}{\bar{z}^2}$	0.25
$\frac{1}{\rho_w \cdot \bar{z}}$	0.75	$\frac{1}{\rho^2_w}$	0.55

Initial examination revealed a high correlation between R_{exp} and ln q_s, as summarized in Fig. 2. However, considerable variability is evident. To try to reduce this variability by including only those lakes likely to be oligotrophic and to which P loadings probably had not undergone recent changes, data from those lakes whose inflowing P concentration was ≤ 25 μg/liter were analyzed further. Table 3 summarizes the correlations and the correlation coefficients for the 20 lakes selected.

For these lakes, the highest correlation existed between R_{exp} and ln q_s (Fig. 3, $r = -0.92$). Note that slightly more than half the lakes used for these correlations were used by Kirchner and Dillon (1975). A least squares linear fit to the data provided the relationship:

$$R_{exp} = 0.86 - 0.143 \ln q_s. \tag{5}$$

The observation that R_{exp} correlated better with areal water loading than with hydraulic washout coefficient (Kirchner and Dillon 1975) is also supported by the results presented in Table 3. However, if values for Lakes Raven and Talbot are excluded as outliers, a high correlation is obtained between R_{exp} and ln ρ_{ic} (Fig. 4, $r = -0.91$). The best fit linear regression equation was

$$R_{exp} = 0.482 - 0.112 \ln \rho_w. \tag{6}$$

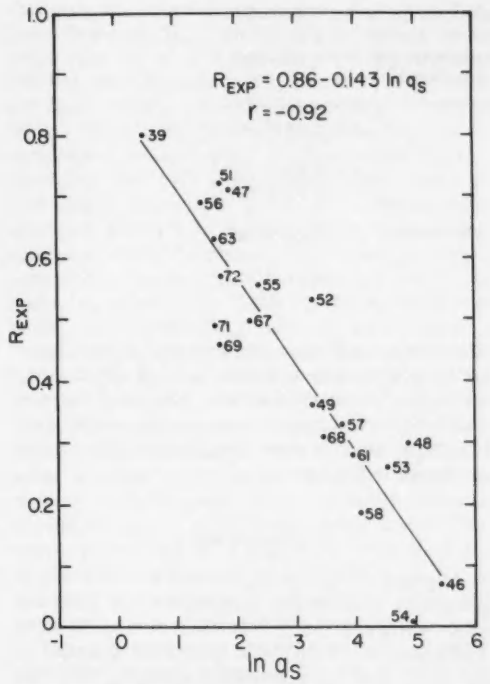

FIG. 3. Regression of R_{exp} on ln q_s for lakes whose $[\bar{p}]$ was $\leqslant 25$ μg/liter (Table 2).

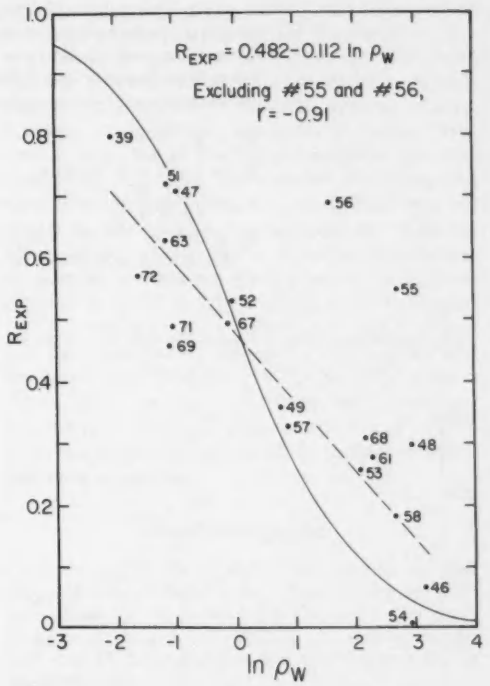

FIG. 4. Regression of R_{exp} on ln ρ_w for lakes whose $[\bar{p}]$ was $\leqslant$ 25 μg/liter (Table 2). Dashed line is regression equation excluding Raven (No. 55) and Talbot (No. 56). Solid line is a graph of $R_p = \frac{\sigma_p}{\sigma_p + \rho_w}$ for $\sigma_p = 1.0$ yr^{-1}.

Raven and Talbot are the shallowest lakes ($\bar{z}$ = 0.73 and 0.85 m, respectively) in the data set so perhaps this relationship between R_{exp} and ln ρ_w is not valid for extremely shallow lakes. Dillon and Rigler (1974), testing a simple phosphorus mass balance model, reported that predicted and observed P values differed markedly for Lakes Raven and Talbot.

Although equations (5) and (6) provide a good fit to observations, they predict R_p greater than 1 for low values of q_s (<0.36 m/yr) or ρ_w (<0.01 yr^{-1}) and R_p less than 0 for high values of q_s (>395 m/yr) and ρ_w (>74 yr^{-1}). For example, equation (6) predicts R_p = 1.22 for Lake Tahoe. Predictions of $R_p < 0$ or > 1 are contrary to limnological experience except in unusual circumstances, thus equations (5) and (6) are not entirely adequate.

Figure 4 also includes a graph of $R_p = \frac{\sigma_p}{\sigma_p + \rho_w}$ for σ_p = 1.0 yr^{-1} to compare the data spread with the shape of a theoretical R_p vs ln ρ_w curve (at σ_p = 1.0 yr^{-1}). For ln $\rho_w > 0$ the curve evidently underestimates observed values of R_{exp} and overestimates observed values for ln $\rho_w < 0$.

Because σ_p and ρ_w seemed related, ln σ_p was regressed on ln ρ_w. Direct measures of σ_p are not available for these lakes. Therefore, σ_p was determined as $\frac{\rho_w \cdot R_{exp}}{1 - R_{exp}}$ (Dillon and Rigler 1974). Data for lakes Tahoe and Superior were included because they provided data points at extremely low values of ρ_w, but lakes Raven and Talbot were excluded. The relationship

$$\ln \sigma_p = \ln 0.761 + 0.472 \ln \rho_w \qquad (r = 0.84) \quad (7)$$

or

$$\sigma_p = 0.761\ \rho_w^{0.472}$$

resulted. Substituting into $(R_p = \frac{\sigma_p}{\sigma_p + \rho_w})$ and simplifying provided an equation of the form

$$R_p = \frac{1}{1 + \alpha \rho_w^{\beta}} \qquad (8)$$

where $\alpha = 1.3$ and $\beta = 0.4$.

TABLE 4. Summary of various relationships between R_p and ρ_w or q_s for 20 selected lakes (indicated by asterisks in Table 2). The correlation coefficients (r) in parenthesis are values obtained when lakes Superior and Tahoe are deleted.

$R_p = \frac{1}{1 + \rho_w^{1/2}}$	$r = 0.94\ (0.91)$
$R_p = 0.482 - 0.112 \ln \rho_w$	$r = 0.93\ (0.91)$
$R_p = \frac{11.73}{11.73 + q_s}$	$r = 0.93\ (0.89)$
$R_p = 0.426e^{(-0.271\ q_s)} + 0.574e^{(-0.00949\ q_s)}$ (Kirchner and Dillon 1975)	$r = 0.94\ (0.90)$
$R_p = 0.854 - 0.142 \ln q_s$	$r = 0.94\ (0.91)$

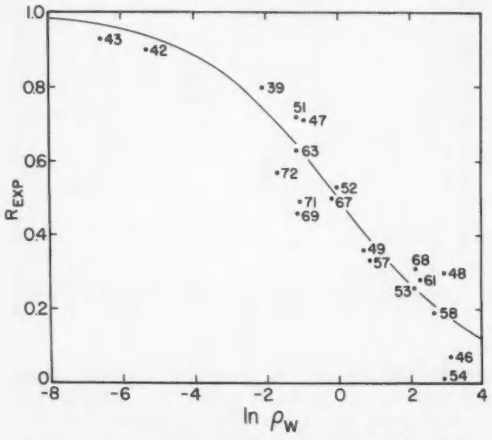

FIG. 5. Comparison of solution of $R_p = \frac{1}{1 + \rho_w^{1/2}}$ with R_{exp} for lakes whose $[\bar{p}]$ was $\leqslant 25$ μg/liter. Raven and Talbot have been excluded; Tahoe ($[\bar{p}]$) = 100 μg/liter) and Superior ($[\bar{p}]$) = 40 μg/liter) have been added.

The coefficients α and β were also estimated using a Gauss–Newton nonlinear least squares algorithm available from the Oregon State University Computer Library. The best estimate for α was 1.12 and for β, 0.49. Thus, equation (8) can be approximated by the expression (Fig. 5):

$$R_p = \frac{1}{1 + \rho_w^{1/2}} (r = 0.94). \qquad (9)$$

The best fit value for v (from equation 4) was 11.73 m/yr ($r = 0.93$), which is slightly lower than that presented by Chapra (1975) or Dillon and Kirchner (1975).

The solutions of these two expressions do not produce values of $R_p < 0$ or > 1 for extremely high and extremely low values of ρ_w or q_s as do several of the previous expressions.

Table 4 summarizes the various expressions that relate the P retention capacity to lake properties. Expressions presented are all based upon water flow normalized to lake size, as either surface area or volume, the lake attributes that seem to control the P retention coefficient to the greatest degree in these lakes.

Discussion

A graph of $[\bar{p}]$ vs. R_p is another way of expressing a relationship between trophic state and those variables thought to control trophic state. Vollenweider (1968) first proposed a graph of L_p vs. $\bar{z}$ and later modified it as L_p vs. $\bar{z}/\tau_w$ ($= q_s$; $\tau_w = \rho_w^{-1}$ = hydraulic retention time) (1975); Dillon (1975) suggested $L_p(1 - R_p)/\rho_w$ vs. $\bar{z}$, which develops directly from the steady state solution of Vollenweider's mass balance model ($[P]_\infty = L_p(1 - R_p)/\rho_w \cdot \bar{z}$; Dillon and Rigler 1974). The graph of $[\bar{p}]$ vs. R_p combines these terms in a different manner so that the vertical axis, $[\bar{p}]$, incorporating both P supply and water flow, represents a potential lake P concentration or trophic state. It is the concentration that would be attained if P acted as a conservative substance in lakes. This potential concentration differs from that defined by Edmondson (1961) which is the phosphorus volumnar loading, J/V. The horizontal axis expresses all those processes affecting the ability of lakes to assimilate that potential as an incorporation of P in the sediments. The relative positions of lakes on a graph of $[\bar{p}]$ vs. R_p is the same as on a $L_p(1 - R_p)/\rho_w$ vs. $\bar{z}$ graph because both graphs are based upon the same concepts and express the same information. We found it more convenient to separate those processes affecting potential lake P concentration (phosphorus supply relative to water supply) occurring external to the lake from those characteristics exhibited by a lake which control sedimentation of P, expressed by R_p.

A comparison of lakes Superior and Zurichsee

illustrates the relative importance of $[\bar{p}]$ and R_p. Lake Superior ($R_{exp} = 0.9$, $[\bar{p}] = 40$ μg/liter, mean lake P = 3–5 μg/liter) is oligotrophic (Beeton and Chandler 1966; Patalas 1972; Dobson et al. 1974), while Zurichsee ($R_{exp} = 0.25$, $[\bar{p}] = 40$ μg/liter, [P] = 32 μg/liter at vernal circulation) is eutrophic (Vollenweider 1968). Assuming that both lakes approximate a steady state, Lake Superior's ability to assimilate incoming P allows it to manifest oligotrophic characteristics while Zurichsee's much lower assimilatory ability dictates that the same $[\bar{p}]$ results in eutrophic conditions. Lake Superior probably could absorb a 40–50 μg/liter increase in $[\bar{p}]$ and remain oligotrophic, while a similar increase in $[\bar{p}]$ for Zurichsee probably would aggravate an already eutrophic problem. Slight changes in Zurichsee's assimilatory capacity would only slightly affect the steady state P concentrations, while a slight reduction in Superior's retention capacity — for example, from 0.9 to 0.8 — could double the steady state lake concentration. This sensitivity of lakes with high R_p to changes in R_p suggests that a careful determination of R_p is necessary if the results of influent P changes are to be reasonably predicted for these lakes.

The equations summarized in Table 4 show that most of the variability in the P retention capacity of these lakes can be accounted for by variation in water flow normalized to a measure of lake size, as ρ_w or q_s. The values predicted from these equations might provide an upper limit for R_p because lakes that were likely to be oligotrophic were intentionally chosen to generate the relationships. No attempt has been made to quantify the probable reduction R_p due to increased productivity. Other factors such as lake morphometry, climate, or lake chemistry could also influence R_p, and a more thorough investigation is necessary to determine these effects.

If loading and flow data are available, the expression of trophic characteristics in terms of $[\bar{p}]$ and R_p not only allows a rapid assessment of trophic state, but also provides a preliminary guide useful for management decisions. Effects of alternatives such as loading reduction or nutrient dilution can be expressed as changes in $[\bar{p}]$. Furthermore, the effect of manipulations affecting R_p, if quantifiable in terms of R_p, can be assessed. Thus, the results of nutrient inactivation or hypolimnetic aeration might be determined as increases in R_p and, therefore, as reductions in steady state P levels. In addition, the effect of combined treatments can be predicted through their changes in $[\bar{p}]$ and R_p.

The $[\bar{p}]$ vs. R_p graph is another way of expressing the relationship between trophic state and variables controlling trophic state. It develops from a continuity equation for P (equation [1]) and can be derived from Vollenweider-type mass balance models. Mass balance models of this nature are intended to describe general characteristics of phosphorus dynamics in lakes. Thus, annual averages of the input variables and rate coefficients are used and results are compared with average conditions in lakes. This type of model has been used to explain existing conditions (Vollenweider 1969, 1975) or to predict changes as a result of reducing P supplies to lakes (Sonzogni et al. 1974; Sonzogni and Lee 1974; Megard 1970). Slightly more complex mass balance models developed by Imboden (1973, 1974) and Snodgrass and O'Melia (1975) might provide a closer fit to average conditions and, more importantly to seasonal changes in lake P. However, the models require further testing to ascertain their generality.

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Recruitment Mechanisms of Southern Gulf of St. Lawrence Atlantic Herring (*Clupea harengus harengus*)

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WINTERS, G. H. 1976. Recruitment mechanisms of southern Gulf of St. Lawrence Atlantic herring (*Clupea harengus harengus*). J. Fish. Res. Board Can. 33: 1751–1763.

Estimates of abundance of the southern Gulf of St. Lawrence herring complex by cohort analysis indicate that both biomass and population fecundity were reduced to low levels in the late 1950s following a widespread fungus disease in the mid-1950s. As a result of two strong year-classes in the late 1950s, however, abundance increased dramatically up to 1964 but has declined continuously since then due mainly to subsequent poor recruitment. Mackerel were also at low levels of abundance in the late 1950s and remained so until the mid-1960s when a series of strong year-classes produced a rapid increase in abundance to the extent that mackerel replaced herring as the dominant pelagic fish in the southern Gulf ecosystem. Changes in herring recruitment, growth, and maturation rates are investigated in relation to changes in herring biomass and total pelagic (herring + mackerel) biomass. Density-dependent changes in all three parameters have occurred in herring; mackerel also have interacted with the growth and recruitment of southern Gulf herring. This suggests that the carrying capacity of the southern Gulf for pelagic fish is limited and that competition and predation by mackerel intensifies the logistic response of herring. Thus, recruitment of southern Gulf herring in the period under consideration was largely controlled by the total pelagic biomass, acting mainly through herring up to the mid-1960s and through mackerel since then. The increase in mackerel abundance is attributed to a combination of favorable temperature regime and optimum spawning biomass. That being so, the probability of large year-classes of herring in the near future will depend heavily on the interaction between favorable survival conditions for mackerel and the effectiveness of ICNAF regulations to maintain mackerel biomass at maximum recruitment levels.

WINTERS, G. H. 1976. Recruitment mechanisms of southern Gulf of St. Lawrence Atlantic herring (*Clupea harengus harengus*). J. Fish. Res. Board Can. 33: 1751–1763.

Les estimations d'abondance du complexe du hareng du golfe Saint-Laurent méridional par analyse des cohortes démontrent que la biomasse et la fécondité de la population ont été toutes deux réduites à de bas niveaux vers la fin des années 1950, à la suite d'une maladie à fongus qui se répandit parmi la population au milieu des années 1950. Deux fortes classes d'âge vers la fin des années 1950, cependant, contribuèrent à une augmentation dramatique d'abondance jusqu'en 1964. Mais il y eut déclin continu par la suite dû en grande partie à un faible recrutement. Le maquereau se trouvait également à de bas niveaux d'abondance à la fin des années 1950. Il en a été ainsi jusqu'au milieu des années 1960, alors qu'une série de fortes classes d'âge produisirent une augmentation rapide d'abondance, au point que le maquereau remplaça le hareng comme espèce pélagique dominante dans l'écosystème du Golfe méridional. On étudie les changements dans le recrutement, la croissance et les taux de maturation du hareng en relation avec les changements dans la biomasse du hareng et dans la biomasse pélagique (hareng + maquereau) totale. Des changements liés à la densité dans les trois paramètres se sont produits chez le hareng; il y eut également interaction entre le maquereau et la croissance et le recrutement du hareng du Golf méridional. Ceci donne à croire que la capacité de charge de poissons pélagiques du Golfe méridional est limitée, et que la compétition et la prédation par le maquereau intensifient la réponse logistique du hareng. Nous concluons que le recrutement du hareng du Golfe méridional durant la période sous étude était en grande partie contrôlé par la biomasse pélagique totale, par l'intermédiaire surtout du hareng jusqu'au milieu des années 1960 et par celle du maquereau depuis. On attribue à une combinaison de températures favorables et de biomasse reproductrice optimum l'augmentation dans l'abondance du maquereau. Dans ce cas, la probabilité d'obtenir d'abondantes classes d'âge de hareng dans un avenir rapproché dépendra fortement de l'interaction entre des conditions de survie favorables pour le maquereau et de l'efficacité des règlements de l'ICNAF à maintenir la biomasse du maquereau à des niveaux de recrutement maximum.

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THE southern Gulf of St. Lawrence (hereinafter referred to as the southern Gulf or Area T; Fig. 1) is a major spawning area for both spring- and fall-spawning herring (Jean 1956; Day 1957). Tagging experiments (Winters 1970, 1975; Beckett 1971) have confirmed the hypothesis of Hodder (1969) that these herring emigrate in late fall to overwinter in fjords along the western half of the south coast of Newfoundland (hereinafter referred to as southwest Newfoundland or Area J; Fig. 1) and reenter the southern Gulf in late April–early May to spawn and feed. Prior to 1965, annual landings from the southern Gulf stock complex of herring averaged less than 40,000 metric tons (Tibbo et al. 1969; Hourston and Chaulk 1968) and tended to reflect demand for the product rather than abundance of the resource. This situation changed rapidly after 1965 when purse-seining was initiated on substantial quantities of overwintering herring along southwest Newfoundland and by 1967 the mobile purse-seine fleet had expanded their activities to include nearly all months of the year and various areas of the southern Gulf. Such multiple seasonal fisheries resulted in a dramatic rise in landings to nearly 300,000 metric tons in 1970 (Winters and Hodder 1975), declining to less than 50,000 metric tons in 1973. The increase in abundance of southern Gulf herring was due to the accumulation of biomass produced by a succession of strong year-classes of herring spawned in the fall of 1958 and spring of 1959; the equally rapid decline was due to the succession of poor year-classes during the 1960s (Winters and Hodder 1975).

The southern Gulf is also a major spawning and feeding area for mackerel (Sette 1950; MacKay 1967) and together with herring form the major portion of the pelagic fish biomass in that area. Major changes in the abundance of southern Gulf herring have occurred since the late 1950s; historical records indicate that mackerel also undergo dramatic changes in abundance (Sette and Needler 1934; Taylor et al. 1957). Since both mackerel and herring are important pelagic predators and have common food preferences (Moores et al. 1975; MacKay 1967), fluctuations in abundance of mackerel may have played a significant role in the observed changes in herring production.

Since 1972 the southern Gulf stock complex of herring has been managed by the Atlantic Herring Management Committee on the basis of catch restrictions and various qualitative conservation measures. As an advisor to that Committee, the author undertook the following analyses of the recent variations in recruitment of southern Gulf herring with the ultimate objective of increasing both short- and long-term predictability of abundance changes.

Materials and Methods

The basic data used to calculate biomass and recruitment levels of southern Gulf herring for the period 1965–71 were obtained from Winters and Hodder (1975) and for 1972 and 1973 from Winters and Parsons (1972) and from data on file at the St. John's Biological Station. Tibbo et al. (1969) provides monthly catch data and commercial length frequencies of nominal catches of herring in Area T during the period 1958–64. Since Area J represents only a part of ICNAF Division 3P, catch statistics for the herring fishery in this area were derived from detailed statistical records on file at the St. John's Biological Station. Utilizing age-length keys and age-specific weights (Hodder et al. 1972), age-compositions of herring catches in Areas T and J during 1958–64 have been derived. In accordance with the recommended convention of ICNAF (Hunt et al. 1973) age-groups have been used instead of ages. Thus a fish is placed in age-group 0 in the year of its birth, regardless of whether it was spawned in the spring or autumn, and both types enter the next age-group at the same time of the year. In this context the fishery year pertains to annual catches during the 12-mo period from April of one year to March of the next.

Population numbers of each age-group of spring- and fall-spawning herring of the southern Gulf stock complex were calculated for each fishery year by sequential computation using cohort analysis (Pope 1972) from the numbers caught at each age-group. Cohort analysis is a modified form of "virtual" population analysis based on a rearrangement of the Baranov (1918) catch equation approximated by the following formula:

$$N_i = C_i e^{M/2} + N_{i+1} e^{M}$$

where N_i = population of a cohort at the i^{th} year
C_i = catch of a cohort at age i
N_{i+1} = population size at the beginning of the $(i+1)^{th}$ year
M = instantaneous coefficient of natural mortality

$N_{i+1} = N_t$ where t represents the last age-group of a year-class for which catch data are available. N_t is calculated from the Baranov (1918) catch equation as follows:

$$N_t = \frac{C_t Z_t}{F_t(1 - e^{-Z_t})}$$

where C_t = last year's catch of a cohort
F_t = instantaneous coefficient of fishing mortality in the last year for which catch data are available (terminal F).
Z_t = instantaneous coefficient of total mortality in year t ($Z_t = F_t + M$).

Cohort analysis, as with other "virtual" population methods, has the advantages of providing estimates of population size and fishing mortality rates inde-

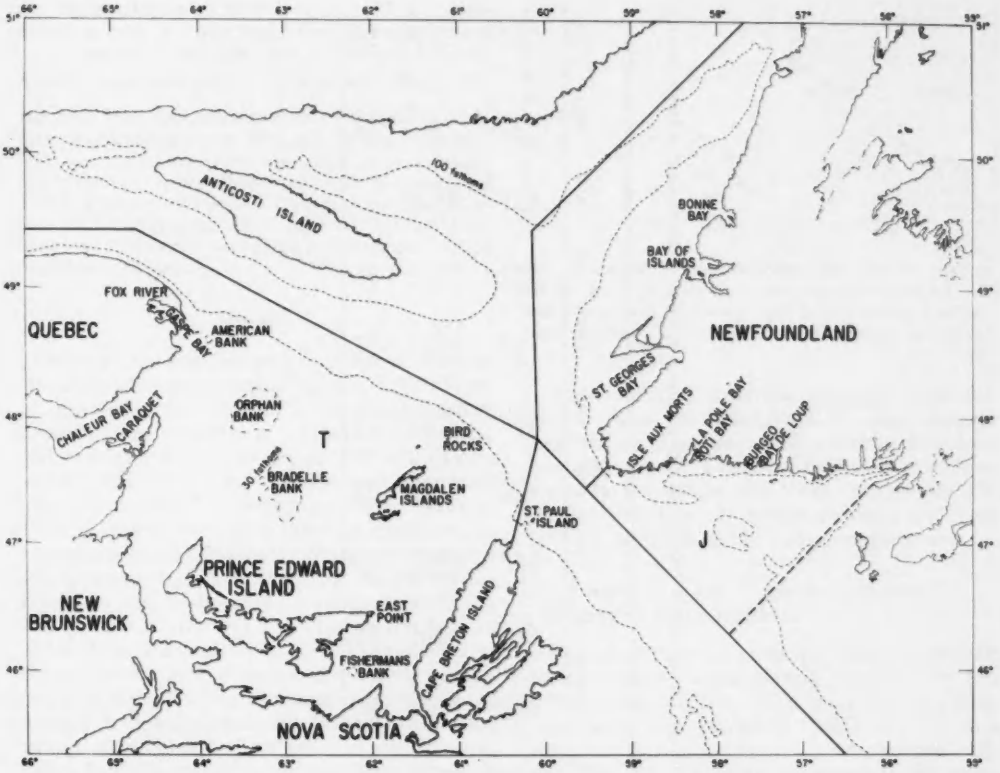

FIG. 1. Southern Gulf of St. Lawrence (Area T) and southwest Newfoundland (Area J) showing locations mentioned in the text.

pendent of effort data, and of providing increasingly accurate estimates of population size as a year-class passes through the fishery. It is, however, sensitive to errors in M and F_t; a review of the effects of errors in these parameters is provided by Pope (1972).

For the period 1965–73 an estimated value of $M = 0.20$ (Winters and Hodder 1975) and starting values of F_t derived from relative changes in annual fishing effort levels (Winters and Hodder 1975) were used in the above formulae to calculate stock sizes. Prior to the development of the purse-seine fishery in 1965 effort data were not available; for this period $M = 0.2$ and terminal fishing mortality rates (F_t) equal to the 1965 level of F for each spawning group (Winters and Hodder 1975) were assumed.

Age-specific fecundities have been estimated from fecundity–length relationships of spring- and fall-spawning herring given in Hodder (1972), utilizing age-length keys contained in Hodder et al. (1972). From such data the total egg production of each spawning group (population fecundity) has been calculated based on population estimates by age from cohort analysis.

With the exception of rough estimates of spawning stock size from egg production levels (MacKay 1973), data on biomass levels of mackerel in the southern Gulf are scanty. However, Moores et al. 1975 have concluded from comparisons of various biological characteristics and evaluation of both recent and historical tagging experiments that the mackerel that belong to the so-called northern "contingent" (Sette 1950), having as its major spawning area the southern Gulf, contribute substantially to the landings from an intensive international fishery for mackerel during their overwintering period in the offing of New England (ICNAF Subareas 5 and 6). An analytical assessment of this fishery combined with data from mackerel fisheries as far north as Newfoundland (ICNAF Subarea 3) (Anderson 1975) provides estimates of recruitment values and biomass levels of mackerel for the period 1968–75. These estimates, however, do not include significant quantities of mackerel caught by recreational fisheries in Canada and the United States (32,000 metric tons in the U.S. alone in 1970 (Anderson 1975)) and thus are undoubtedly underestimates of the total mackerel biomass. The analytical estimate of total mackerel biomass in 1968 agrees well with estimates by MacKay (1973) of spawning stock size in the southern Gulf in 1968, thus supporting the above conclusion

TABLE 1. Stock sizes by number (N_s) and weight (W_s), year-class strength (at age-group 2) (R_t), and egg production (E) of southern Gulf Atlantic herring (*Clupea harengus harengus*) 1958–73.

Spawning group	Fishery year															
	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Spring-spawners:																
$R_t(\times 10^{-6})$	483	3455	783	154	410	330	145	154	189	92	575	55	125	160	?	?
$N_S(\times 10^{-6})$[a]	825	828	1098	4298	4249	3510	3152	2787	2270	1890	1516	1031	1173	787	620	607
$W_S(\times$ ' on m tons)[a]	149	146	170	442	632	671	646	604	528	455	363	244	196	135	117	115
$E(\times 10^{-12}$ eggs)	16.1	16.1	16.0	17.3	31.3	66.2	65.9	68.3	64.7	59.3	47.1	31.3	22.4	13.0	12.9	13.1
Autumn-spawners:																
$R_t(\times 10^{-6})$	7132	1988	1026	641	1379	1629	788	739	496	800	326	161	710	340	?	?
$N_S(\times 10^{-6})$	1152	1746	8535	8947	8321	7431	7439	7604	6947	6234	5297	4585	3325	2126	1938	1743
W_S('000 m tons)	111	159	472	750	1073	1198	1228	1226	1200	1152	1043	834	601	387	272	247
$E(\times 10^{-12}$ eggs)	8.7	11.7	16.0	22.1	25.4	52.2	159.8	213.1	219.6	202.7	185.2	178.0	131.6	75.7	45.8	42.7
Autumn + spring:																
$N_S(\times 10^{-6})$	1977	2574	9633	13245	12570	10491	10591	10391	9721	8124	6813	5616	4498	2913	2558	2350
W_S('000 m tons)	260	305	642	1192	1705	1869	1874	1830	1728	1607	1406	1078	797	522	398	362

[a]Age-group 2 and older.

and the conclusion of Moores et al. (1975). Consequently trends in these population parameters have been considered representative of the mackerel in Area T. Stock sizes refer to midyear levels $\frac{(B_t + B_{t+1})}{2}$ and have been back-calculated to 1965 from ICNAF data; abundance levels in 1963 and 1964 were derived from pro-rating the 1965 analytical estimate using U.S. research vessel abundance indices (Anderson 1975). Prior to 1963 annual Canadian catches (MacKay 1973) (assuming effort relatively stable) have been used to pro-rate abundance estimates derived for the subsequent year.

Results

Both spring- and fall-spawning herring were at low levels of biomass during the late 1950s (Table 1), apparently as a result of a fungus disease that caused severe mortality in southern Gulf herring and mackerel during the period 1953–57 (Tibbo and Graham 1963) and resulted in a substantial drop in landings (Templeman 1966; MacKay 1973; Tibbo et al. 1969). Herring increased in abundance during the early 1960s as a result of strong recruitment from the 1958 and 1959 year-classes of fall- and spring-spawners, respectively, and peaked at nearly 1.9 million metric tons in 1964. After the mid-1960s herring abundance in the southern Gulf commenced to decline, particularly after 1968 as the purse-seine fishery expanded both temporally and spatially to include nearly all months and all areas in the southern Gulf. By 1973 the total biomass of both spawning groups was lower than in any year since 1959.

In 1958 the biomass of spring-spawners, which had traditionally supported the bulk of herring landings in Area T prior to the mid-1950s (Tibbo et al. 1969), was only marginally more abundant than that of fall-spawners. This supports the observations of Tibbo and Graham (1963) that the fungus that depleted the southern Gulf populations in the mid-1950s was primarily evident in spring-spawning herring. Table 1 indicates that with the recruitment to the stock of the large 1958 year-class at age 2 in 1960, fall-spawners became dominant and continued to remain so up to 1973.

The large 1959 year-class of spring-spawners was over 4 times as strong as the next strongest year-class (1960) (Table 1), 6 times as strong as the strongest year-class (1968) in that group since 1960, and over 60 times as strong as the weakest year-class (1969). Amongst autumn-spawners the extremely large 1958 year-class was twice as large as the largest year-class of spring-spawners (1959), 3.5 times as large as the next strongest year-class of autumn-spawners (1959), 9 times stronger than the strongest year-class (1967) since 1964, and over 44 times stronger than the weakest year-class (1969). For both spawning groups average recruitment has been generally low during the 1960s, being only 8% of the 1959 level in spring-spawners and only 11% of the 1958 level in autumn-spawners.

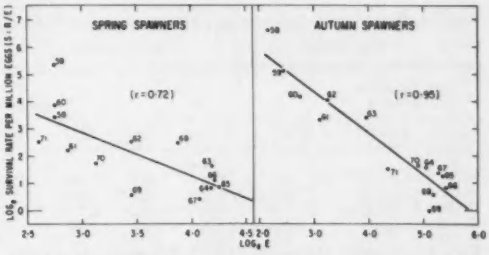

FIG. 2. Relationship between the rate of recruitment (survival rate per unit egg production) and egg production of spring- and fall-spawning southern Gulf Atlantic herring (*Clupea harengus harengus*).

EGG PRODUCTION AND SURVIVAL RATES OF SOUTHERN GULF HERRING

Egg production of both spawning components of the southern Gulf herring was at very low levels during the late 1950s when the two large year-classes were produced (Table 1), rose to a peak in the mid-1960s, but then declined substantially. By 1972 the spring-spawning component had been reduced to its lowest level of egg production and population size since 1958. The autumn-spawning component had also been reduced to a low level of egg production and stock size by 1972 but that level was still above that of the late 1950s.

Survival rates per unit egg production, calculated as the ratio of recruitment strength at age-group 2 to the egg production 2 yr earlier, have been plotted against egg production and the relationship analyzed by log-log regression (Fig. 2). The highly significant negative correlations in both spawning groups indicates that substantial density-dependent compensation in survival rate may occur in response to changes in egg production. The unusually high survival rates associated with the 1958 and 1959 cohorts of fall- and spring-spawners, respectively, allowed very large year-classes to be produced from extremely low levels of egg production.

Recruitment of southern Gulf herring during the period 1958–70 is plotted against parent stock size (egg production) in Fig. 3 and the relationship fitted by eye. The scatter diagram

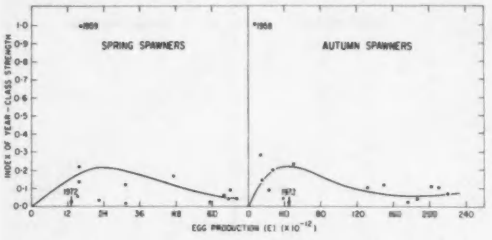

FIG. 3. Scatter diagram (fitted by eye) of stock–recruit relationship of southern Gulf herring, 1958–70.

indicates that large egg production may be inhibitory rather than conducive to the production of strong year-classes. Of greater significance is the fact that egg production levels equivalent to those that produced the anomalously larger 1958 and 1959 year-classes have subsequently resulted in the production of weak cohorts. This suggests that factors other than parent stock size, i.e. density-independent factors, are affecting the recruitment of southern Gulf herring and that these factors have changed since the late 1950s. Thus the stock recruit curves in Fig. 3 may not be particularly relevant in predicting year-class strength from egg production levels.

DENSITY-DEPENDENT CHANGES IN GROWTH AND MATURITY OF SOUTHERN GULF HERRING

Major changes in population levels such as observed in southern Gulf herring during the period 1965–73 may sometimes be accompanied by density-interactive changes in growth and maturity (Hile 1936; MacGregor 1964; Iles 1968; Pitt 1975). Data on mean length- and mean weight-at-age of southern Gulf herring for the period 1965–73 are available from Hodder et al. (1972) and from unpublished information on file at the St. John's Biological Station. The younger age-groups in the exponential part of the growth curve have been selected as most likely to reflect density-dependent growth changes. There is a general increase in mean length-at-age (Table 2) and mean weight-at-age (Table 3) for both spring- and fall-spawning herring from 1965 to 1973. The difference between the period of high abundance of southern Gulf herring (1965–69) and low abundance (1970–73) was greater in autumn-spawners (4.0% in length, 13.0% in weight) than in spring-spawners (2.0% in length, 5.7% in weight).

To evaluate the degree of density-dependence of herring growth apparent in Tables 2 and 3 regressions of mean length and mean weight against herring biomass (age-group 2 and older) were calculated for each spawning group (Fig. 4).

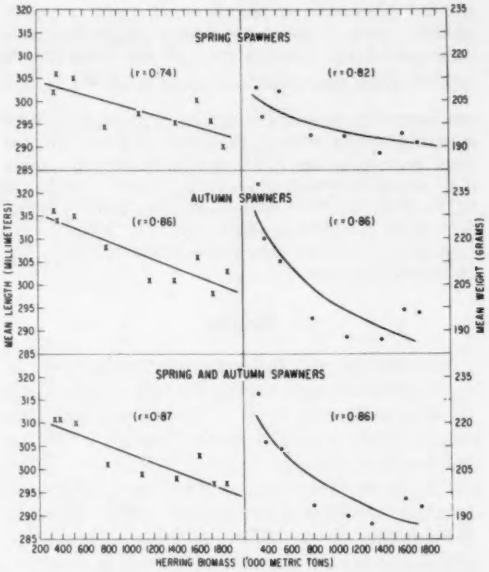

FIG. 4. Regressions of mean length and mean weight of southern Gulf herring against changes in herring biomass, 1965–73.

Significant negative correlations were obtained for both spawning groups when changes in mean weights and mean length were compared with changes in biomass levels of southern Gulf herring, suggesting that density-dependence of growth is occurring. For both size variables, correlation coefficients are higher in fall-spawners than in spring-spawners. This is consistent with evidence of density-dependence since fall-spawners are much more abundant than their spring counterparts.

The acceleration in growth rate during the 1970s is also reflected in the increase in maturation rates of both spring- and fall-spawners (Table 4). This increase in maturation rate and corresponding decrease in mean age-at-maturity is more pronounced in fall-spawners, which is in line with the greater change in growth of that component.

Biomass levels of mackerel and herring during the period 1958–73 are shown in Fig. 5. Both mackerel and herring were at low levels of abundance during the late 1950s, apparently as the result of the fungus disease. Herring increased in abundance during the early 1960s as a result of strong recruitment; the mackerel biomass and recruitment remained at a low level until the mid-1960s after which strong recruitment, particularly from the 1967 year-class, produced a rapid rise in abundance when the herring re-

TABLE 2. Mean length-at-age by spawning group of southern Gulf herring sampled in southwest Newfoundland and Area T, 1965–73.

Spawning group	Age-group	Mean length (*mm*)									Unweighted mean length	
		1965	1966	1967	1968	1969	1970	1971	1972	1973	1965–69	1970–73
Spring-spawners	3	257	275	282	268	273	246	283	282	280	271.0	272.8
	4	288	294	298	293	293	297	287	298	296	293.2	294.5
	5	301	299	308	303	306	313	316	308	307	303.4	311.0
	6	315	314	312	314	316	320	333	334	323	314.2	327.5
	Total	1161	1182	1200	1178	1188	1176	1219	1222	1206	1181.8	1205.8
	Unweighted mean (ages 3–6)	290.3	295.5	300.0	294.5	297.0	294.0	304.8	305.5	301.5	295.4	301.5
Fall-spawners	4	276	257	282	271	271	274	295	288	294	271.4	287.8
	5	298	302	300	296	298	309	303	303	314	298.8	307.3
	6	315	313	316	311	313	320	329	323	323	313.6	323.8
	7	321	321	325	325	322	329	334	343	333	322.8	334.8
	Total	1210	1193	1223	1203	1204	1232	1261	1257	1264	1206.6	1253.7
	Unweighted mean (ages 4–7)	302.5	298.3	305.8	300.8	301.0	308.0	315.3	314.3	316.0	301.7	313.4
Autumn + spring	Weighted mean[a] (ages 3–7)	298.5	207.5	303.9	298.7	299.7	303.4	311.4	311.4	311.2	299.6	309.5

[a]Weighted according to relative abundance of each spawning group.

TABLE 3. Mean weight-at-age by spawning groups of southern Gulf herring samples along southwest Newfoundland and in Area T, 1966–73.

Spawning group	Age-group	Mean weight (*g*)								Unweighted mean weight	
		1966	1967	1968	1969	1970	1971	1972	1973	1966–69	1970–73
Spring spawners	3	150	146	133	147	143	155	142	162	144	151
	4	180	194	185	183	174	179	190	203	186	187
	5	205	205	204	208	217	231	211	225	206	221
	6	230	230	229	236	240	268	253	245	231	252
	Total	765	775	751	774	774	833	796	835	767	811
	Unweighted mean (ages 3–6)	191	194	188	194	194	208	199	209	192	203
Autumn-spawners	4	150	164	151	141	144	173	168	187	152	168
	5	189	180	179	184	181	173	207	233	183	199
	6	218	209	191	203	215	243	234	255	205	237
	7	222	230	225	222	230	263	269	284	225	262
	Total	779	783	746	750	770	852	878	959	765	866
	Unweighted mean (ages 4–7)	195	196	187	188	193	213	220	240	192	217
Autumn + spring	Weighted mean (ages (3–7)	194	196	187	190	193	211	213	230	192	210

[a]Weighted according to relative abundance of each spawning group.

source was declining due to weak recruitment and heavy fishing. USA indices of mackerel abundance from research vessel surveys confirm the trends in mackerel abundance described above (Fig. 5, lower half). Also, age compositions of mackerel catches from ICNAF Subarea 3 to Statistical Area 6 in 1968 (Anon. 1975) following a period of very light exploitation contained less than 3.5% fish 7 yr old and older, whereas in 1974 after a period of heavy exploitation these

TABLE 4. Maturation rates and mean age-at-maturity of spring- and fall-spawning herring sampled in southwest Newfoundland during the fishery periods 1965–69 and 1970–72.

Spawning group	Age-group	1965–69 No. imm.	1965–69 No. mat.	1965–69 % mat.	1970–72 No. imm.	1970–72 No. mat.	1970–72 % mat.
Spring-spawners	2	18	—	0.0	11	2	15.4
	3	13	2	1.3	197	45	18.6
	4	16	54	77.1	43	164	79.2
	5	40	202	83.5	1	754	99.9
	6	6	313	98.1	—	>500	100.0
	7	—	>500	100.0	—	>500	100.0
Age at 50% maturity				3.8			3.5
Fall-spawners	2	—	—	0.0	—	—	0.0
	3	5	—	0.0	10	—	0.0
	4	59	1	1.7	81	6	6.9
	5	174	22	11.2	54	15	21.7
	6	173	332	65.7	3	51	94.4
	7	19	809	97.7	—	118	100.0
	8	—	>500	100.0	—	>500	100.0
Age at 50% maturity				5.9			5.2

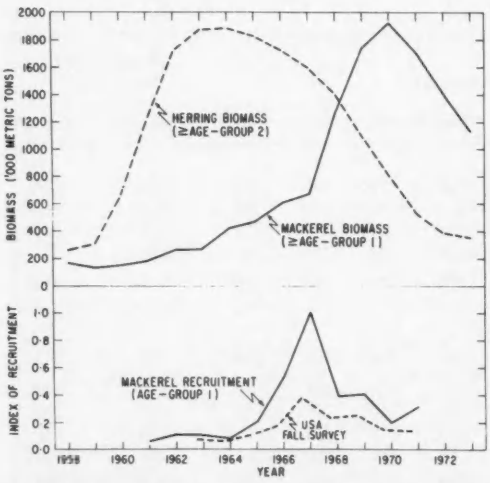

FIG. 5. Trends in herring and mackerel abundance in the southern Gulf of St. Lawrence, 1958–73. Subordinate figure shows relative mackerel recruitment.

age-groups comprised nearly 14% of the total catch, thus substantiating the low level of mackerel abundance and recruitment in the late 1950s and early 1960s. Since 1970 the mackerel biomass has been declining, primarily as a result of huge landings by the international fleet off the New England area (over 380,000 metric tons in both 1972 and 1973). Nevertheless, since the late 1960s mackerel have replaced herring as the dominant pelagic species in the Gulf of St. Lawrence.

INTERACTION OF MACKEREL WITH RECRUITMENT AND GROWTH OF SOUTHERN GULF HERRING

The changes in growth and recruitment of southern Gulf herring documented above occurred simultaneously with an upsurge in mackerel abundance. Mackerel and herring have common preferences for a number of important prey species, particularly euphausiids (Moores et al. 1975) and mackerel are also known to prey on herring larvae (B. S. Muir personal communication) and herring eggs. The significance of such interactions of mackerel on herring growth and recruitment have therefore been analyzed using stepwise multiple regression (Draper and Smith 1966).

Trends in mean length and mean weight (Tables 2 and 3) of southern Gulf herring (spring- and autumn-spawners combined) in relation to changes in herring biomass and total (herring + mackerel) pelagic biomass in Area T during 1965–73 are shown in Fig. 6. Rather than showing a pattern of continuous increase corresponding to the monotonic decline in herring biomass, the growth of southern Gulf herring follows more closely the variation in the total pelagic biomass. The general relationship among these variables was best described by the following multivariate regression equations (Fig. 7)

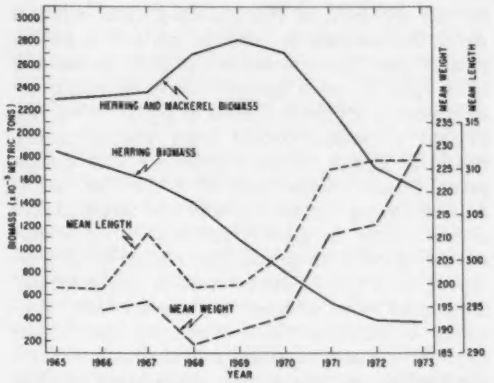

FIG. 6. Relationship between trends in mean length and weight (spring- and fall-spawners combined) of southern Gulf herring and changes in herring biomass and total pelagic (herring + mackerel) biomass.

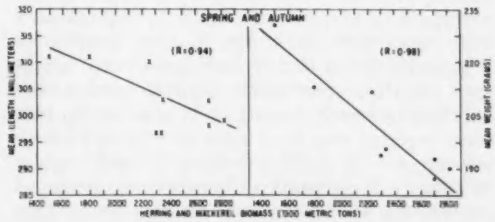

FIG. 7. Regressions of mean length and mean weight of southern Gulf herring against the combined herring and mackerel biomass, 1965–73.

(HB = herring biomass; MB = mackerel biomass):

$$\bar{W} = 265.2 - 0.033\ HB - 0.024\ MB \quad (1)$$

$$\bar{L} = 322.7 - 0.012\ HB - 0.006\ MB \quad (2)$$

Dep. variable	Indep. variable	Coeff.	Stand. partial reg. coeff.
$\bar{W}$	HB	−0.033	−1.23
$\bar{W}$	MB	−0.024	−0.77
$\bar{L}$	HB	−0.012	−1.19
$\bar{L}$	MB	−0.006	−0.54

The F-values for both equations were highly significant. The proportion of explained variation (R^2) in length by the addition of mackerel biomass to the herring biomass ($R^2 = 0.88$) is significantly greater than that explained by herring biomass alone ($r^2 = 0.76$); similarly the addition of mackerel biomass to herring biomass substantially increased the amount of explained variation

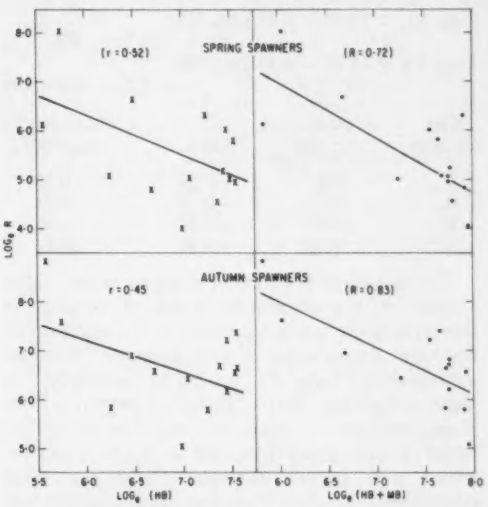

FIG. 8. Relationship between recruitment of southern Gulf herring and herring biomass and combined herring and mackerel biomass for the year-classes 1958–71.

in weight from 74 to 96%. This strongly suggests that the carrying capacity of the southern Gulf for herring and mackerel is limited and that the competition for common food items by these species has depressed the growth of herring. Although there is no unique statistical test of the relative importance of particular variables in multivariate regression analyses, standard partial regression coefficients indicate that herring biomass has a much greater effect on herring growth than mackerel biomass. This is not unreasonable since mackerel compete for only a subset of the total food spectrum of herring.

From the late 1960s to 1973 the total pelagic (herring and mackerel) biomass in the southern Gulf declined by more than 40% (Fig. 6) implying commensurate increase in nominal ration size available to herring. Over this period, however, average weight of herring (age-groups 3–7) increased by only 21% perhaps reflecting a decline in gross growth efficiency (Log K) with increase in ration size as predicted by Paloheimo and Dickie (1966).

Multiple regression analyses have also been carried out to evaluate the effects of mackerel on recruitment of spring- and fall-spawning herring in the Gulf of St. Lawrence during the period 1958–73 (Fig. 8). The general relationship among these variables was best described by the following multivariable regression equations.

$$\text{Log}_e R_{as} = 12.69 - 0.29 \text{ Log}_e \text{HB} - 0.65 \text{ Log}_e \text{MB} \quad (3)$$

$$\text{Log}_e R_{ss} = 12.63 - 0.54 \text{ Log}_e \text{HB} - 0.54 \text{ Log}_e \text{MB} \quad (4)$$

Dep. variable	Indep. variable	Coeff.	Stand. partial reg. coeff.
R_{as}	HB	−0.29	−0.22
R_{as}	MB	−0.65	−0.74
R_{ss}	HB	−0.54	−0.35
R_{ss}	MB	−0.54	−0.52

The F-values for both equations were highly significant. The amount of explained variation in recruitment of spring-spawners by the addition of mackerel biomass to herring biomass increased substantially from 27 to 52%; similarly for autumn-spawners the addition of mackerel biomass increased the explained variation in recruitment of that group from 20 to 69%. This, together with higher standard partial regression coefficients, suggests that the total pelagic biomass in the southern Gulf, acting in large part through predation by mackerel, has exerted a controlling influence on the magnitude of herring recruitment at least over the period of investigation.

Discussion and Conclusions

Winters and Hodder (1975) have shown that the great abundance of herring in the southern Gulf and southwest Newfoundland during the 1960s was derived mainly from the accumulation of biomass produced, by two large year-classes spawned in the autumn of 1958 and in the spring of 1959. Apparently such dominant year-classes were produced under exceptional circumstances occurring in succession after a fungus disease (*Ichthyosporidium hoferi*) had caused widespread mortalities of both herring and mackerel in the southern Gulf during 1953–57. Since the late 1950s recruitment to the southern Gulf stock complex of herring had declined steadily which, coupled with a strong recruitment of mackerel in the late 1960s, has resulted in the replacement of herring by mackerel as the most abundant pelagic fish resource in the southern Gulf of St. Lawrence.

A large volume of literature has been published on a wide variety of factors associated with fluctuations in fish recruitment; in general, such factors may be classified into three types: a) stock–recruit or logistic response in which the internal dynamics of the population acts in a compensatory manner to prevent it from expanding to infinity or declining to extinction. The stock–recruit relationship is generally considered to take the form of either a flat-topped curve in which recruitment is constant beyond a certain critical level (asymptotic model of Beverton and Holt (1957)) or a kurtotic curve in which recruitment is inversely related to parent stock size beyond a certain critical level (compensatory model of Ricker [1954, 1958]); b) interspecific predation and competition. If competition is important among the adult stocks one might expect to see effects on growth rate with concomitant effects on maturation rate and fecundity (Nikolsky et al. 1973). Survival rate is not generally considered to be affected in the short term. Predation usually has direct effects on fish recruitment by reducing larval survival and would be expected to be most intense when large juvenile and adult predator biomass levels are present; c) environmental factors which through density-dependent effects tend to overlay fluctuations in recruitment caused by (a) and/or (b).

Data presented here suggest that all three classes of effects may have contributed to the variations in herring recruitment in the southern Gulf since the late 1950s. Logistic control of population size is clearly indicated by the significant negative correlations between recruitment and herring biomass and growth and herring biomass implying that there must be a limited carrying capacity for herring in Area T which results in increased predation of larvae and increased competition for food at large biomass levels. This effect is also evident in the general form of the stock–recruit diagrams which, although exhibiting wide scatter, correspond reasonably well with the compensatory models of Ricker (1954, 1958). Egg production and herring biomass were at low levels during the late 1950s but this should have assured low larval production. This was apparently the case, since larval survival rate per unit egg production was at its highest level during this period. Egg production peaked in the mid-1960s when survival rates and recruitment were at their lowest levels. An improvement in survival rates per unit egg production is evident during the late 1960s as egg production and biomass levels declined.

Interactive changes in growth and maturity have been noted in southern Gulf herring, apparently in partial response to changes in herring biomass, but more in relation to both herring and mackerel biomass. This suggests that in the southern Gulf carrying capacity for pelagic fish must be defined for more than herring alone, at least in the adult stages and that competition by mackerel intensified the logistic growth response of herring. The increase in the amount of explained variation in herring recruitment when the total

pelagic (herring and mackerel) biomass is considered and the significant negative correlation between mackerel biomass and herring recruitment supports empirical studies (B. S. Muir personal communication) that predation of herring larvae by mackerel is occurring in the southern Gulf. Thus during the late 1950s the attrition in the pelagic fish biomass in the southern Gulf due to disease must have substantially reduced predation on herring larvae to the extent that a large vacuum was created in the carrying capacity producing conditions which were amenable to the production of unusually large year-classes of herring. These same large year-classes built up the pelagic biomass during the early 1960s causing a decline in herring recruitment. The strong recruitment of mackerel during the late 1960s maintained the pelagic biomass at high levels at a time when the herring biomass was declining due to recruitment failure and developing fisheries. Consequently the expected logistic increase in herring recruitment during the late 1960s was not forthcoming despite low abundance levels of adult fish. In short, recruitment of southern Gulf herring in the period under consideration was controlled by the total pelagic biomass, acting mainly through herring up to the mid-1960s and through mackerel since then.

According to Sutcliffe (1972, 1973) the St. Lawrence River runoff, by virtue of its control on estuarine entrainment and nutrient transfers, plays a dominant role in determining annual variations in primary and secondary productivity in the southern Gulf. Annual runoff levels of the St. Lawrence River during the period under consideration have shown wide fluctuations (Sutcliffe 1972). The effects of this environmental signal on recruitment of southern Gulf herring were analyzed by multiple stepwise regression. For spring-spawners the coefficient of multiple determination (R^2) increased only 1% whereas R^2 for fall-spawners increased 4%. These small increases in the explained variation in herring recruitment suggest that either runoff is not the appropriate environmental parameter or that other factors, cited above, have had a more direct effect.

The ability of mackerel to take advantage of favorable survival conditions at a time when herring recruitment remained depressed may be explained by the reproductive biology of mackerel. Mackerel are warmwater fish requiring a high temperature range for spawning (11–18 C, Worley 1933) and their abundance on the Atlantic coast of Canada has shown wide fluctuations apparently in response to temperature trends (Templeman 1966; Taylor et al. 1957). Unlike

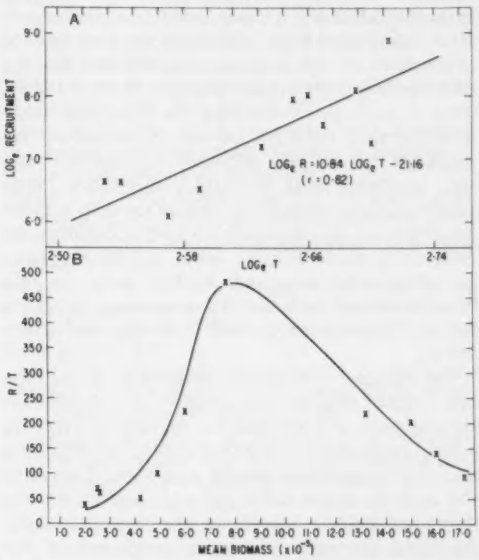

FIG. 9. A, Log-log regression of mackerel recruitment against average surface temperature (June–August) at Entry Island, southern Gulf for the year-classes 1961–71; B, relationship between mackerel recruitment per unit temperature (R/t) and mean mackerel biomass ($\geqslant$ age-group 1).

herring, mackerel are pelagic spawners and as such are much less restricted in their spawning areas than herring that have a high specificity with regard to substrate conditions.

To assess the effect of temperature on the recent increase in mackerel abundance, regression analyses have been carried out between mackerel recruitment and surface temperature at Entry Island, Quebec (Lauzier and Hull 1969) averaged for the months covering the spawning and development of mackerel eggs and larvae (June–August) (Fig. 9A). A significant ($P < 0.05$) possitive correlation is obtained, confirming earlier observations (Taylor et al. 1957) that temperature plays an important role in determining mackerel abundance and distribution. The effect of stock size on mackerel recruitment, adjusted for variations in temperature, is shown in Fig. 9B. Mackerel recruitment is evidently also dependent upon stock size, being greatest at biomass levels between 700,000–900,000 metric tons. Thus, despite the low levels of pelagic fish (mackerel + herring) biomass in the southern Gulf in the late 1950s, mackerel recruitment remained low due to a combination of unfavorable temperatures and small spawning stocks. Considering both parameters, temperature is probably the more critical factor affecting

mackerel abundance since, whatever the parent stock size, spawning will be restricted by the availability of high temperatures required for egg development and larvae survival (Worley 1933). Thus in periods of warming the spawning range and carrying capacity of the environment for mackerel larvae will increase substantially and this, combined with the highly migratory (Sette 1950) nature of mackerel, enable them to prevent development of local high density conditions by emigrating to and using what would otherwise be fringe spawning and feeding areas around Newfoundland and the Atlantic coast of Nova Scotia (Moores et al. 1975; Stobo and Hunt 1974).

On balance therefore, apparently during the late 1960s factors responsible for recruitment success were unfavorable for herring of Area T, whereas conducive conditions existed for mackerel and this recruitment success of mackerel explains the fact that mackerel replaced herring as the dominant pelagic species in the southern Gulf. Applying this same reasoning to stocks of the future the probability of large year-classes of herring will depend heavily on the interaction between favorable survival conditions for mackerel and the efficacy of ICNAF regulations to maintain the mackerel biomass at maximum recruitment levels.

Acknowledgments

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Origin and Characteristics of "Fall-Run" American Shad (*Alosa sapidissima*) from the St. John River, New Brunswick

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GABRIEL, W. L., W. C. LEGGETT, J. E. CARSCADDEN, AND B. D. GLEBE. 1976. Origin and characteristics of "fall-run" American shad (*Alosa sapidissima*) from the St. John River, New Brunswick. J. Fish. Res. Board Can. 33: 1764–1770.

American shad (*Alosa sapidissima*) taken from the St. John River, New Brunswick, during the fall of 1973 were studied to determine river of origin and duration of residence in the river. One-way analyses of variance and classification by discriminant function analysis of meristic characters suggested that most of these shad were part of the St. John River population. Fat and water content of the fish, maturity, and stomach contents suggested that the movement into the estuary was recent and not a spawning migration.

GABRIEL, W. L., W. C. LEGGETT, J. E. CARSCADDEN, AND B. D. GLEBE. 1976. Origin and characteristics of "fall-run" American shad (*Alosa sapidissima*) from the St. John River, New Brunswick. J. Fish. Res. Board Can. 33: 1764–1770.

On a fait des études sur l'alose savoureuse (*Alosa sapidissima*) de la rivière Saint-Jean, Nouveau-Brunswick, à l'automne 1973 dans le but de déterminer la rivière d'origine et la durée de résidence dans la rivière. Des analyses unidirectionnelles de la variance et une classification par analyse discriminante des fonctions des caractères numériques suggèrent que la plupart de ces aloses font partie de la population de la rivière Saint-Jean. La teneur en gras et en eau des poissons, la maturité et les contenus stomacaux donnent à croire que le mouvement d'entrée dans l'estuaire est récent et n'est pas une migration de fraie.

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REGULAR occurrence of subadult and/or adult American shad (*Alosa sapidissima*) in the estuary of the St. John River, New Brunswick, during the late summer and early fall is well known to local residents. To our knowledge no similar phenomenon occurs in other Atlantic coast rivers supporting shad populations. The timing of their appearance, which occurs well after the annual spawning migration has ended, and the reported robust condition of the fish, which differ greatly from the emaciated, spent, downstream migrants, suggests the existence of a fall movement of shad into the river from the Bay of Fundy.

These shad could be part of the St. John River population or, alternatively, of a heterogeneous aggregation of shad from U.S. and Canadian rivers known to concentrate in the Gulf of Maine during late summer and early fall (Talbot and Sykes 1958) in response to seasonal cycles of ocean warming and cooling (Leggett and Whitney 1972). Penetration of this group into the upper Bay of Fundy has been demonstrated by tagging experiments: shad tagged in Chesapeake Bay, along the coast of New Jersey, in the Connecticut River, and in the St. Lawrence estuary have been recovered near the mouth of the St. John River in the upper Bay of Fundy (Leggett and Whitney 1972; Leim and Scott 1966; Talbot and Sykes 1958). Thus, periodic penetration to any area of the St. John River below the saltwater interface by members of this heterogeneous group based in the Gulf of Maine could explain the occurrence of shad in the estuary.

In this study we attempted to determine whether or not this group of "fall-run" shad is of a single geographical origin, and to assess the probable duration of its residence in the river.

Materials and Methods

Twenty-nine shad were collected between September 29 and October 2, 1973 as an incidental catch from an experimental salmon trap operated by Environment Canada and located at Westfield, New Brunswick, approximately 17 km upstream from the mouth of the St. John River (Fig. 1). The estuary to Westfield is tidal and has a layer of saline water 15–20‰ at depths of 10 m with surface salinities as high

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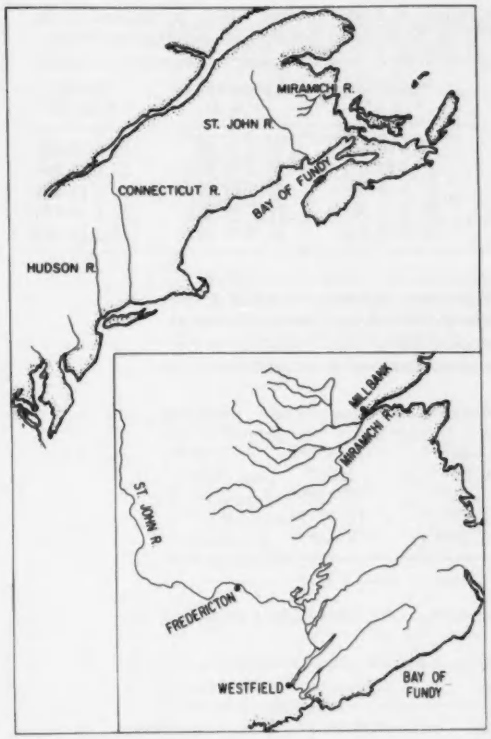

FIG. 1. Study areas on Atlantic coast and in St. John and Miramichi rivers.

as 5‰. Zooplankton of the estuary are mainly of Bay of Fundy and Gulf of Maine origin (Trites 1960). These facts would indicate that the shad were captured in salt water. All specimens were frozen within 1–2 h of capture and kept frozen until analysis was begun.

Geographical origin of the group was evaluated through analysis of meristic characters. Dorsal, anal, and right pectoral fin rays, and anterior and posterior scutes were counted for each fish following methods employed by Hill (1959) and Carscadden and Leggett (1975a). Means of meristic counts were compared by one-way analysis of variance with means of identical characters from discrete spawning populations of shad in the Hudson, Connecticut (Hill 1959), Miramichi, and St. John rivers (Carscadden and Leggett 1975a). Meristic counts of the St. John River population, which is composed of a number of subpopulations (Carscadden and Leggett 1975a, b) were not available. Thus, to obtain means of meristic counts for shad in the St. John River as a whole we weighted and combined counts from three subpopulations (Kennebecasis River, Washademoak Lake, and Mactaquac Dam) of shad spawning in the St. John River (Carscadden and Leggett 1975a). Only shad captured at Millbank, at the mouth of the river, were used in the Miramichi River sample. In addition, stepwise discriminant analysis (Dixon 1975) was used to compare the meristic characters of the Westfield sample with those of the four Atlantic coast populations.

Duration of river residence was estimated by comparing fat and water content of visceral and somatic tissues in the Westfield sample with corresponding values for shad sampled at the initiation and termination of the freshwater spawning migration in the Connecticut and St. Johns (Fla.) rivers (B. D. Glebe and W. C. Leggett unpublished data). Adult shad do not feed in fresh water, therefore, fat reserves are depleted in direct relation to the duration of the freshwater residence. Homogenates of viscera were prepared by grinding all visceral material in a Lourdes blender until a uniform consistency was reached. Homogenates of body tissue were made by grinding the whole body in a large capacity Waring blender. A subsample was then ground until a uniform paste was obtained. Homogenates were frozen for storage. Two samples of each homogenate were weighed and dried at 90 C for at least two days, and reweighed to determine moisture content. Fat content of these dried samples was determined using the method of Korn and Macedo (1973).

Previous spawning history was determined by scale readings (Cating 1953; Judy 1961). Gonads were removed and visually examined to assess the general state of sexual maturity.

Results

MERISTIC ANALYSIS

Mean meristic counts for fish in the Westfield sample are presented in Table 1, together with comparable counts for shad from the St. John, Miramichi, Connecticut and Hudson river populations. One-way analyses of variance showed that individual meristic characteristics of the Westfield sample differed significantly from those of the St. John River population only in anal fin-ray number. When compared with the Hudson river population the sample differed in the pectoral and dorsal fin-ray number (Table 2), and when compared with the Miramichi and Connecticut River populations the Westfield sample differed significantly in all but the anal fin-ray count (Table 2). There were no significant differences in meristic characters between males and females in the Westfield sample.

Discriminant functions for the St. John, Miramichi, Connecticut, and Hudson rivers, based on the five meristic characters described, are given in Table 3. Bartlett's test for homogeneity of variances (Sokal and Rohlf 1969) yielded significant heterogeneity as did the *F*-max test (Sokal and Rohlf 1969). Strength of classification based on

TABLE 1. Means and SE (in parentheses) of meristic characters of American shad (*Alosa sapidissima*) in the Westfield sample, and for shad populations from the St. John, Miramichi, Connecticut, and Hudson Rivers.

Meristic character	Westfield $N = 29$	St. John $N = 588$	Miramichi $N = 159$	Connecticut $N = 91$	Hudson $N = 104$
Dorsal fin rays	18.3 (0.14)	18.0 (0.05)	17.6 (0.06)	17.2 (0.09)	17.9 (0.08)
Anal fin rays	21.5 (0.20)	21.8 (0.07)	21.3 (0.07)	21.2 (0.10)	21.6 (0.09)
Pectoral fin rays	16.3 (0.16)	16.2 (0.05)	15.9 (0.05)	14.7 (0.09)	15.8 (0.07)
Anterior scutes	22.1 (0.11)	22.2 (0.05)	22.4 (0.06)	21.6 (0.07)	22.0 (0.06)
Posterior scutes	15.6 (0.12)	15.5 (0.06)	16.1 (0.06)	14.9 (0.09)	15.3 (0.08)

TABLE 2. *F* values for one-way analysis of variance comparing means of meristic characters of the Westfield sample with those of the St. John, Miramichi, Connecticut, and Hudson rivers' shad populations. $*P > 0.05$; $**P < 0.05$; $***P < 0.01$.

Meristic character	St. John	Miramichi	Connecticut	Hudson
Dorsal fin rays	1.92*	17.09***	34.45***	4.46**
Anal fin rays	4.40**	0.34*	1.06*	0.70*
Pectoral fin rays	0.06*	6.83***	77.45***	9.98***
Anterior scutes	0.67*	11.25***	12.27***	0.05*
Posterior scutes	0.13*	10.33***	17.64***	2.63*

TABLE 3. Coefficients of discriminant functions* for St. John, Miramichi, Connecticut and Hudson rivers' shad population.

Variable	St. John	Miramichi	Connecticut	Hudson
V_1	26.94936	26.34792	25.48834	26.73401
V_2	19.06264	18.59915	18.65709	18.84816
V_3	35.44273	34.74864	31.98215	34.49879
V_4	44.35745	44.95474	43.34990	44.06804
V_5	27.68620	26.60254	26.50587	27.30687
K	−1447.37280	−1443.25635	−1319.40918	−1411.50171

*$Y = A_1V_1 + A_2V_2 + \ldots + A_5V_5 + K$, where A_1, A_2 etc. = coefficient 1, 2, ... , 5, V_1 = dorsal fin ray, V_2 = anal fin ray, V_3 = pectoral fin ray, V_4 = anterior scute, V_5 = posterior scute, K = constant.

these functions is thus reduced. However, Isaacson (1954) notes that linear discriminant functions computed from uncommon variance–covariance matrices based on large sample size give good results. An *F*-matrix calculated to assess the significance of differences between rivers based on these functions indicated significant differences between all populations except the Hudson and St. John rivers (Table 4). Carscadden and Leggett (1975a) previously reported no significant difference between the Hudson River population and the Mactaquac Dam subpopulation of the St. John River based on discriminant function analysis.

A posteriori classifications (Dixon 1975) designed to test the ability of these four individual discriminant functions to assign individual fish to their respective populations are presented in Table 5, together with the most probable assignment of the 29 fish from the Westfield sample to the four reference populations. Percentage of correct classifications were St. John River 51%; Miramichi River 66.4%; Connecticut River 79.1%; and Hudson River 39.4%. The majority (65.5%) of the Westfield specimens were assigned to the St. John River, with a maximum of 17.2% being assigned to any one of the remaining rivers. Coefficients for canonical variables were also computed (Dixon 1975) and the first canonical variable was plotted against the second (Fig. 2) to give an optimal two-dimensional illustration of the separation of the groups. The similarity of the Westfield and St. John River samples is obvious.

TABLE 4. *F* matrix showing significance of differences between four Atlantic coast shad populations based on discriminant functions (df = 5,690; $^{**}P < 0.01$).

	St. John R.	Miramichi R.	Connecticut R.
Miramichi R.	31.52*		
Connecticut R.	109.82*	96.70*	
Hudson R.	8.98	21.01*	41.83*

TABLE 5. A posteriori assignment of individual shad sampled from the St. John, Miramichi, Connecticut, and Hudson rivers to a population based on the stepwise discriminant analysis, and the most probable assignment of the Westfield samples to a reference population.

	Assignment			
Source	St. John	Miramichi	Connecticut	Hudson
St. John	303	131	19	135
Miramichi	20	106	10	23
Connecticut	1	3	72	15
Hudson	30	17	16	41
Westfield	19	5	2	3

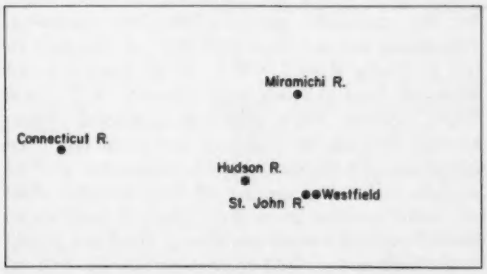

FIG. 2. Plot of the first canonical variable against the second canonical variable to illustrate the relative similarity between American shad (*Alosa sapidissima*) populations examined. Distance between points is proportional to the degree of similarity in the variables measured.

SPAWNING HISTORY

Scale analyses indicated that 79% of the Westfield sample had never spawned, while the balance had spawned 1 or more times previously (Table 6). The sex ratio of the sample was approximately 50:50 and the spawning history of the two sexes was similar.

Appearance of the gonads was similar in all specimens. All gonads were deep red in color and extended about one-half the length of the body cavity, generally occupying less than one quarter of its volume. Eggs were not distinguishable to the naked eye, but were visible under 10× magnification.

STOMACH CONTENTS

All stomachs were opened and examined under the microscope. No identifiable organisms were observed but the majority of stomachs contained a quantity of pink material suggesting recent feeding.

FAT AND MOISTURE CONTENT

Mean visceral and body fat, and moisture content of the 29 Westfield shad separated by sex are presented in Table 7 together with corresponding values for male and female shad captured in the Connecticut and St. Johns (Fla.) rivers at the time of entry into fresh water and near the termination of their spawning migration (B. D. Glebe and W. C. Leggett unpublished data). Mean fat content was slightly higher in the Westfield sample than in fish from the Connecticut and St. Johns (Fla.) rivers captured during entry into the river from the sea. Fat values in the Westfield sample were much higher than fat values for shad sampled near the termination of their freshwater migration.

Mean moisture values were approximately equal to those observed in fish recently entering rivers, and consistently lower than those of fish following a prolonged river residence.

TABLE 6. Age distribution and number of previous spawnings of American shad (*Alosa sapidissima*) sampled at Westfield, N.B.

Age	No. females	No. males	Total	% of sample
2	0	1	1	3.5
3	8	8	16	55.2
4	3	4	7	24.1
5	2	1	3	10.3
6	1	1	2	6.9
No. previous spawnings	No. females	No. males	Total	% of sample
0	12	11	23	79.4
1	1	2	3	10.3
2	1	1	2	6.9
3	0	0	0	0.0
4	0	1	1	3.4

Discussion

Use of meristic characters to classify shad populations assumes constant and significant differences between stocks. Such differences have been demonstrated (Carscadden and Leggett 1975a; Nichols 1966) and used previously to classify shad as belonging to one of two different river populations (Fischler 1959). These differences apparently result from the combination of accurate homing in shad at the river (Hollis 1948; Judy 1961; Vladykov 1950; Walburg and Nichols 1967) and the tributary levels (Carscadden and Leggett 1975a, b; Nichols 1966). The use of discriminant function analysis for separating individuals into two or more populations is well developed (Bilton 1972; Fischler 1959; Fukuhara et al. 1962; Hill 1959; Mais 1972; Messieh 1975; Parsons 1972; Royce 1964).

Our analysis of meristic characters in four Atlantic coast populations and the Westfield sample indicates that the most probable river of origin of the group of 29 shad samples at Westfield was the St. John River, N.B. This conclusion, based on the results of one-way analyses of variance and stepwise discriminant analysis, suffers from the facts that meristic data from all Atlantic coast shad populations were not available for comparison, and that the St. John River discriminant function was constructed from three tributary populations. In spite of this the Westfield sample resembled the St. John River sample more closely than any other. The similarity of the Westfield and St. John samples, and the dissimilarity with the other populations tested, especially when analysed by discriminant function analysis, gives support to our conclusion regarding the origin of the Westfield sample.

High somatic and visceral fat content of individuals in the Westfield sample clearly eliminates the possibility that these shad had spent a significant period upriver in fresh water or that the six shad which had previously spawned were recent outmigrants which had remained in fresh water for an extended period following spawning. (Spawning occurs from mid-May to mid-July in the St. John River, N.B.). Adult shad do not normally feed in fresh water (Leach 1925; Leim 1924; Nichols 1959), although occasional opportunistic feeding on hatching fly larvae has been observed (Chittenden 1969). Atkinson (1951) suggested that the absence of food in adult shad stomachs resulted from their physical inability to collect available food organisms. Shad are planktonic feeders and feed mainly on mysids (10–30 mm) while at sea (Leim 1924). The largest freshwater plankton are copepods (maximum size approximately 5 mm) and these are apparently too small to be effectively filtered. In addition, W. C. Leggett and B. D. Glebe (unpublished data) have observed feeding to be greatly depressed or absent in the estuarine portion of the spring spawning migration. River residence is thus characterized by a rapid reduction in fat reserves accumulated at sea, and by a correlated increase in moisture content (B. D. Glebe and W. C. Leggett unpublished data). Higher fat content of the Westfield sample, compared to that of shad collected immediately after entry into the St. Johns (Fla.) and Connecticut rivers during their spawning migration may be indicative of the added energy costs of gonad production experienced by the latter prior to the spawning migration.

Duration of the estuarine residence of the

TABLE 7. Means and SD of body and visceral fat and moisture content for shad in the Westfield collection and shad sampled in the Connecticut and St. Johns (Fla.) rivers immediately after entry into the river and near the termination of their freshwater spawning migration.

	Fat (% wet wt)		Moisture (% wet wt)	
	Mean	SD	Mean	SD
		Westfield		
Females				
Viscera	29.46	8.55	59.16	6.51
Body	21.96	5.63	61.34	3.86
Males				
Viscera	34.03	10.35	34.03	7.93
Body	18.91	4.03	62.69	3.13
		Connecticut River		
Females entering river before spawning				
Viscera	4.67	2.63	75.73	2.01
Body	15.67	1.92	63.48	1.74
Females leaving river after spawning				
Viscera	1.65	1.55	78.15	1.63
Body	11.11	3.18	68.70	2.69
Males entering river before spawning				
Viscera	19.87	6.45	63.85	5.53
Body	17.25	1.96	61.80	1.78
Males leaving river after spawning				
Viscera	8.33	7.47	72.73	2.01
Body	7.79	3.62	70.60	3.28
		St. Johns River (Fla.)		
Females entering river before spawning				
Viscera	18.41	6.29	64.01	4.71
Body	17.98	2.36	60.68	2.28
Females (spent) at spawning grounds				
Viscera	0.61	0.30	82.27	2.33
Body	2.61	2.70	78.27	3.73
Males entering river before spawning				
Viscera	29.16	3.55	55.67	3.30
Body	18.74	1.75	60.14	1.29
Males (spent) at spawning grounds				
Viscera	3.21	2.55	79.71	1.81
Body	3.07	3.06	74.50	2.91

Westfield shad cannot be determined precisely, but we believe it to have been short. As previously noted, the estuary to Westfield is tidal and the salinity measurements (Trites 1960) indicate that salt water is present at least as far upriver as Westfield. There is little local zooplankton production and the zooplankton of the estuary are mainly of Bay of Fundy and Gulf of Maine origin (Trites 1960). Trites found moderate concentrations of zooplankton in the estuary in February and December 1957 and 1958, but reported the entire estuary exhibited an extreme paucity of zooplankton when sampled in May and August.

If the low zooplankton abundance reported by Trites (1960) during spring and late summer is typical, it seems unlikely that the Westfield shad could have obtained sufficient food in the estuary to accumulate high fat reserves, or to maintain these reserves for prolonged periods after their accumulation while feeding actively at sea.

The early state of development of gonads in the shad in the Westfield sample clearly rules out the possibility of a fall spawning population of shad in the St. John system. Presence of virgin and mature (previously spawned) fish in the sample adds support to Talbot and Sykes (1958) suggestion that juveniles and adults occur and move together at sea.

Our conclusion, based on the foregoing analyses, is that the occurrence of adult (and subadult) shad in the St. John River in late summer and early fall results from short excursions by fish principally, but not necessarily exclusively, from the St. John River population into the estuary from adjacent feeding areas in the northern Gulf of Maine and the Bay of Fundy. This movement of shad into the St. John River is neither a spawning migration nor a feeding migration but probably represents straying into the estuary from adjacent feeding areas. Furthermore, these fish probably did not experience extra energy costs connected with osmoregulation and adaptation to fresh water since they were captured in salt water. Their disappearance, later in the fall, probably results from movement of the entire Atlantic coast stock into more southerly waters in response to seasonal cooling of ocean waters (Leggett and Whitney 1972).

Acknowledgments

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Effect of Diets Containing Dogfish (*Squalus acanthias*) Meal on the Mercury Content and Growth of Pen-Reared Coho Salmon (*Oncorhynchus kisutch*)

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The use of dogfish (*Squalus acanthias*) meal as a complete replacement for herring or other low mercury (Hg) content fish meal in rations intended for rearing cultured salmon introduces the risk of producing fish that exceed the current U.S. FDA tolerance level of 0.5 ppm Hg. The amount of Hg that accumulates in the muscle is related not only to the total Hg content of the fish, but is probably also related to the form in which it is present in the diet and to other constituents that may react with the Hg in the diet. Our results indicate that dogfish meal may be used as a partial (<50%) replacement for the fish meal portion of the diet without encountering Hg values (in the muscle) that exceed 0.5 ppm Hg. No evidence was found that naturally occurring chelating agents in dehydrated orange peel or polygalacturonic acid–cellulose complexes (PG) have the ability to chelate and prevent the deposition of Hg in either the muscle or the liver of the fish. It was observed that growth is decreased in coho salmon (*Oncorhynchus kisutch*) fed OMP-type diets in which 50% or more of herring meal was replaced with dogfish meal.

SPINELLI, J., AND C. MAHNKEN. 1976. Effect of diets containing dogfish (*Squalus acanthias*) meal on the mercury content and growth of pen-reared coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 1771–1778.

L'emploi de farine d'aiguillat commun (*Squalus acanthias*) comme substitut total de farine de hareng ou autres farines de poisson à faible teneur en mercure (Hg) dans les rations de saumons d'élevage risque de produire des poissons qui dépassent le niveau de 0.5 ppm de Hg présentement toléré par la FDA des E.-U. La quantité de mercure qui s'accumule dans le muscle est non seulement liée au contenu total de Hg dans les poissons, mais elle dépend probablement aussi de la forme sous laquelle le mercure est présent dans le régime et des autres constituants pouvant réagir avec Hg dans le régime. D'après nos résultats, la farine d'aiguillat commun peut être utilisée comme substitut partiel (<50%) de la portion farine de poisson du régime sans produire de valeurs de Hg (dans le muscle) excédant 0.5 ppm de Hg. Nous n'avons pas de preuve que les agents de chélation qui se trouvent naturellement dans les pelures d'orange déshydratées ou dans les complexes acide polygalacturonique–cellulose (PG) sont capables de causer la chélation ou d'empêcher la déposition de Hg soit dans le muscle soit dans le foie des poissons. Nous avons constaté un ralentissement de croissance chez des saumons coho (*Oncorhynchus kisutch*) nourris de régimes du type OMP dans lesquels 50% ou plus de la farine de hareng avait été remplacé par de la farine d'aiguillat commun.

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THE recent upsurge in salmonid aquaculture in the Pacific northwest (Mahnken 1975; Novotny 1975) has been accompanied by nutritional research that is oriented toward producing cost-effective diets for rearing these species to commercial sizes that generally range between 260 and 390 g. Shortages and high prices for fish meal have once again prompted users to investigate the possibility of using dogfish (*Squalus acanthias*) as a source of raw material for meal production. Previous investigations in this area have produced conflicting results regarding the nutritive value of dogfish meal in animal and fish diets (Rhian et al. 1942; Fowler and Banks 1967; Westgate et al. 1964; March et al. 1971; Satia

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TABLE 1. Proximate composition, total mercury, and methylmercury content of dogfish (*Squalus acanthias*) meal added to OMP diets.

Source of dogfish meal	Components					
	Moisture (%)	Protein[a] (%)	Fat (%)	Ash (%)	Total mercury (*ppm*)	Methyl mercury[b] (*ppm*)
Canada Packers (Expt 1)	6.0	62.0	16.7	13.4	2.30	1.88
B&M (Expt 2)	6.2	63.8	19.8	11.1	1.37	1.12

[a]N × 6.25 — no correction made for NPN.
[b]Expressed in terms of mercury.

and Brannon 1975). Those investigators who have reported poor growth results generally attributed their findings to the high urea and other nonprotein nitrogenous constituents of dogfish meal. Others suspect that adverse processing conditions necessitated by the nature of the raw material decrease the nutritive value of the meal. In addition, recent concern with contaminants, particularly mercury (Hg), in human foods may add still another factor to be resolved in assessing whether or not dogfish is a suitable component in animal and fish rations. Dogfish has been reported to contain moderate-to-high amounts of Hg (Childs and Gaffke 1973; Forrester et al. 1972). Whether use of dogfish or other fish meals with high Hg content in commercial salmonid diets could introduce the hazard of producing commercial fish that exceed the recently promulgated US Food and Drug tolerance of 0.5 ppm Hg has yet to be completely resolved. Menasveta (1974) fed rainbow trout (*Salmo gairdneri*) fingerlings diets containing added methylmercury and mercuric chloride and established that Hg was deposited in the muscle and organs of fish fed these diets. He also found that the addition of dehydrated orange peel retarded the deposition of Hg in the fish and attributed these findings to the chelating effect of polygalacturonic acid (and possibly flavones) with the Hg. More recently Satia and Brannon (1975) found increased Hg contents in rainbow trout fingerlings fed on diets containing whole and eviscerated dogfish over those fed diets not containing dogfish.

In this study we attempt to define the limits to which dogfish meal can be included in diets used to rear pan-sized salmon. In two separate experiments diets containing various quantities of dogfish meal were fed to fish for at least 7 mo. The primary objective of these experiments were to determine 1) the relation between the amount of dogfish meal in the diet and the amount of Hg deposited in the muscle and liver of the fish, 2) whether or not the addition of polygalacturonic acid or orange peel affects the deposition of Hg in the muscle and liver, and 3) the relation between growth and the amount of dogfish meal in the diet. The first experiment (Expt 1) was conducted from August 1973 through April 1974. The second experiment (Expt 2) was conducted from May 1974 through December 1974.

Materials and Methods

DIET COMPONENTS AND PREPARATION

The basic control diet used in both experiments was the Oregon Moist Pellet (OMP). This diet contains 28% herring meal and its total composition is described by Halver (1972). In the experimental diets dogfish meal was substituted for the herring meal portion of the diet. The dogfish meal used in Expt 1 was obtained from Canada Packers, Ltd., Vancouver, B.C., and was prepared by the conventional processing technique of cooking, pressing, and flame drying. The dogfish meal used in Expt 2 was obtained from the B & M Company, Bellingham, Washington, and was prepared by cooking dogfish under reduced pressure to remove the water and then pressed to remove the oil. The proximate composition, total mercury, and methylmercury contents of these meals are given in Table 1. The dehydrated orange peel and polygalacturonic acid–cellulose complex were obtained from Sunkist Growers, Ontario, California. One week before the start of the experiments, 91 kg of each diet were prepared as follows:

Expt 1 — 1. Omp control; 2. 100% substitution of the herring meal with dogfish meal; 3. 100% substitution of the herring meal with dogfish meal. 2.5 kg of dehydrated orange peel were added per 47.5 kg of the basic diet; 4. 100% substitution of the herring meal with dogfish meal. 2.5 kg of polygalacturonic acid–cellulose complex (PG) were added per 47.5 kg of the basic diet.

Expt 2 — 1. OMP control; 2. 50% substitution of the herring meal with dogfish meal; 3. 75% substitution of the herring meal with dogfish meal; 4. 100% substitution of the herring meal with dogfish meal.

Soya oil was added to experimental diets 2 and 3 to bring them to an oil content equivalent to diet 4.

Fish

Freshwater growth of all experimental fish was accelerated using 11–12 C water resulting in smoltification at age 0. The fish used in Expt 1 were obtained from the Minter Creek Hatchery, Washington. Those used in Expt. 2 were obtained from the Washington Department of Fisheries Skykomish Hatchery.

Enclosures, Vaccination, and Feeding Regime

Coho salmon (*Oncorhynchus kisutch*) smolts were maintained in small rectangular net pens in the NMFS Aquaculture Experiment Station at Clam Bay, Puget Sound, Washington. The nets were 1.2 × 2.1 × 1.8 m and constructed of knotless nylon webbing with 5-mm mesh apertures. The nets were weighted with rectangular pvc pipe frames filled with sand. Duplicate net pens were maintained for each treatment except for the control diet in Expt 1. Salinity in Clam Bay varies from 27–29‰. Daily seawater temperature in the net pens during the 1973 experiments ranged from 6.8 to 13.3 C and from 8.15 to 15.4 C during the 1974 experiments.

All fish were vaccinated intraperitoneally with heat-killed *Vibrio anguillarum* prior to entry into salt water and after all had smolted. The bacterin was prepared from a strain of *V. anguillarum* commonly found to cause mortality in cultured salmon in Clam Bay (Harrell et al. 1976).

Fish were fed an unrestricted (excess) ration of the moist pellet feed 4 times daily.

Sampling, Weighing, and Measuring

Expt 1 — Growth measurements were made about every 30 days during periods of rapid growth in the summer and fall and about every 60 days in the winter when water temperatures were low and growth was slow.

Fish were fasted for at least 16 h before weighing. On the day of sampling all fish were netted from each pen, placed in a subsampler (Worlund et al. 1969), and a 20% subsample was taken. Fish from the subsample were anesthetized with M.S. 222, measured for fork length, weighed to the nearest 0.1 g, and placed in running sea water for recovery. Those fish not weighed in the subsample were anesthetized, counted into a tank, and bulk weighed on a hanging spring balance.

At each sampling interval eight fish of various weights (randomly selected) were removed from each pen and killed for Hg analysis.

Expt 2 — Growth measurements were taken and fish selected for Hg as in Expt 1 except that all fish from each treatment group were weighed and measured.

Analytical Methods

Mercury analysis — Total mercury content of the muscle and livers was determined by either the method of Munns and Holland (1971) or Malaryandi and Barrette (1970) as modified by Munns (1972). The method of Munns and Holland uses sulfuric, nitric, and perchloric acids for digestion with Na-molybdate as a catalyst. The modified method which uses nitric and sulfuric acids with vanadium pentoxide as a catalyst is more rapid and yields comparable results (Munns 1972). Total mercury in the muscle was determined on 5-g samples. The fish were filleted, comminuted, and an aliquot taken for analysis. The livers from eight fish were composited, comminuted, and the analysis was made on either the entire contents or a 5-g subsample. All analyses for total Hg were done in duplicate.

Methylmercury determinations on the dogfish meals were made on 5-g samples by the method described by Westöö (1967).

Moisture and oil — Ten-gram samples were dried in a vacuum oven (85 C) to a constant weight. Oil was extracted from the dried sample by refluxing for 24 h with methylene chloride.

Protein — Total nitrogen was determined by the Kjeldahl method, Official Method of Analysis (AOAC 1960). Protein was calculated: (N × 6.25).

Ash — Determinations were made by ashing 2–8 g of dry material in SiO_2 crucible for approximately 10 h (or absence of carbon) in a muffle furnace heated to 550 C.

Results and Discussion

Composition of Dogfish Meal and Experimental Diets

The proximate composition of the dogfish meals is shown in Table 1. Both meals have relatively high oil content. Commercial fish meals (made from herring, menhaden, and anchovy) generally contain about 10% oil. The Hg contents of the two dogfish meals are significantly different: the dogfish meal used in Expt 1 contained 2.3 ppm Hg, and the meal used in Expt 2 contained 1.37 ppm. It is noteworthy, however, that the ratio of methylmercury to total mercury was nearly the same for both meals indicating that the method of manufacture does not selectively remove mercury forms.

The proximate composition and Hg contents of the experimental and commercial control diets are given in Table 2. The control diets contained 0.06–0.12 ppm Hg, slightly more protein, and significantly less lipid than the experimental diets. These compositional variations reflect the lower protein and higher lipid contents of the dogfish meal that was used in preparing the experimental diets. The Hg contents of the experimental diets ranging from 0.21 to 0.68 ppm are almost directly proportional to the amount of dogfish meal used in the diet and indicate that the dogfish meal was

TABLE 2. Proximate composition and mercury content of OMP and experimental diets containing dogfish meal.

Rations	Components				
	Moisture (%)	Protein[a] (%)	Fat (%)	Ash (%)	Mercury (*ppm*)
	Expt 1				
OMP (commercial control)	28.3	35.7	10.2	8.9	0.12
OMP — 100% dogfish meal	28.3	34.3	13.2	8.7	0.68
OMP — 100% dogfish meal and 5% orange peel	31.0	32.0	12.5	8.2	0.60
OMP — 100% dogfish meal and 5% PG	30.0	32.3	13.1	8.2	0.60
	Expt 2				
OMP (commercial control)	29.0	35.6	10.3	8.7	0.06
OMP — 100% dogfish meal	30.0	32.0	14.5	8.1	0.40
OMP — 75% dogfish meal	29.5	32.5	14.2	8.3	0.31
OMP — 50% dogfish meal	29.5	33.1	14.4	8.4	0.21

[a]N × 6.25 — no correction made for NPN.

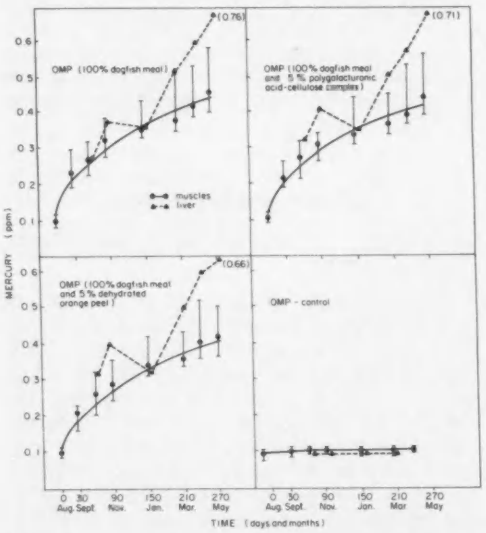

FIG. 1. Accumulation of mercury in the muscle and livers of coho salmon (*Oncorhynchus kisutch*) fed OMP and OMP-type diets in which 100% of the fish meal was substituted with dogfish (*Squalus acanthias*) meal. Effect of adding 5% dehydrated orange peel or 5% PG to these diets on mercury accumulation is also shown (Expt 1).

the only component that contributed to the Hg content of the diet.

ACCUMULATION OF MUSCLE MERCURY

The accumulation of Hg in the muscle and livers of fish from Expt 1 is shown in Fig. 1. For all the experimental diets, there was a rapid accumulation of Hg in the muscle. During the 1st mo of feeding the mean Hg content of the muscle doubled from 0.1 ppm to slightly more than 0.2 ppm. Thereafter, muscle Hg showed a gradual increase in all the fish fed experimental rations. After 180 days of feeding, the Hg values reached approximately 0.4 ppm but none of the individual fish had an Hg level in excess of 0.5 ppm. During the next 60 days, the mean value of Hg concentration increased to approximately 0.45 ppm. During this interval, approximately 15% of the fish contained Hg in the muscle that exceeded 0.5 ppm. At each sampling interval the muscle Hg contents of the fish fed experimental diets containing the dehydrated orange peel and the PG complex were not significantly different from those of the OMP control containing the dogfish meal. After 240 days 15% of these fish also had muscle Hg levels over 0.5 ppm. These results differ from the observation of Menasveta (1974). In his study the absorption and deposition of Hg by rainbow trout from feed containing added methylmercury plus orange peel was significantly lower than from feed containing added methylmercury and no orange peel. This difference can be attributed to the possibility that protein-bound methyl Hg as it exists in fish meal cannot be disassociated by the chelating agents present in dehydrated orange peel, whereas it could have been chelated under the conditions used in Menasveta's experiment. At no time during the experiment did we note a correlation between the size of the fish and Hg content of the muscle. The muscle Hg content of the fish fed the commercial OMP remained constant throughout the experiment indicating a balanced uptake

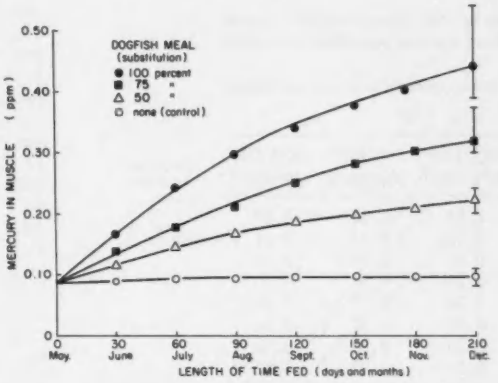

FIG. 2. Accumulation of mercury in the muscle of coho salmon fed OMP and OMP-type diets in which 50, 75, and 100% of the fish meal was replaced with dogfish meal (Expt 2).

and loss of Hg in fish fed diets containing 0.1 ppm Hg.

The accumulation of muscle Hg in the salmon from Expt 2 is shown in Fig. 2. At the 100% level of substitution, the fish showed a similar but more rapid rate of muscle Hg accumulation compared to those observed in Expt 1. After 210 days of feeding, the mean muscle Hg values of the fish were 0.45 ppm, approximately 0.1 ppm higher than those found in Expt 1. At the end of 180 and 210 days, however, only 1 fish of the 32 that were analyzed contained a muscle Hg content of over 0.5 ppm. Fish fed diets at the 50 and 75% levels of dogfish meal substitution for 210 days had mean muscle Hg values of 0.21 and 0.29, respectively. These data show a distinct relation between the amount of Hg that accumulates in the muscle and the amount of Hg in the feed. The rate at which Hg is deposited and is retained in the muscle, however, was not established in this experiment. The fact that Hg was found in similar amounts in fish fed two diets containing different amounts of total Hg suggests that variables other than the form of Hg such as the selenium and cysteine content of the diets could play an important role in this regard. Smith and Armstrong (1975) found abnormally high amounts of Hg in seals with no apparent toxic or pathological effect to the animal and speculated that selenium (which is normally found in high concentrations in most fish) had an attenuating effect on the toxicity of methylmercury by demethylation of the methylmercury to inorganic mercury. These findings became significant to our study because Menasveta (1974) and Sill and Davison (1975) showed that methyl Hg is deposited at a faster rate in the flesh and organs of fish and animals than is inorganic Hg.

Free cysteine has been shown to form soluble complexes with protein-bound mercury in fish muscle (Spinelli et al. 1973). Because of autolysis the cysteine content in meal as well as the form of Hg (Hg complexed with cysteine) in the fish meals could be greatly influenced by the condition of the fish and the processing techniques used to prepare the meal. In this respect Satia and Brannon (1975) found that rainbow trout fry retained more Hg when they were fed diets containing eviscerated dogfish than when fed diets containing whole dogfish, in spite of the fact that the eviscerated dogfish contained 30% less Hg than whole dogfish. This observation is not unlike what we observed in our experiments and lends support to the theory that forms of Hg other than methyl Hg and/or other constituents can influence the rate of uptake and retention of Hg in fish.

ACCUMULATION OF LIVER MERCURY

In Expt 1 the Hg content of the livers was correspondingly higher than the muscle. This was particularly evident after 180 days when Hg content of the livers of fish fed the experimental diets exceeded 0.5 ppm. At the end of 270 days of feeding the Hg content of the livers was approximately 50% higher than the muscle. The decline of the Hg content of the livers from November to January was attributed to feeding a medicated OMP diet containing no dogfish meal for 30 days. In the 1st wk in December (120 days), an outbreak of *V. anguillarum* required that we feed the fish a medicated OMP diet for 30 days. At the next sampling time (January, 150 days), a rapid decline in liver Hg was noted. This may indicate that Hg is rapidly purged from the liver but not from the muscle. This observation is in agreement with Hammond (1971) who reported the half-life of Hg in the muscle of trout to be 7 mo.

In Expt 2 we again found that liver Hg exceeded muscle Hg at each sampling interval (Table 3). At the 50 and 75% levels of dogfish meal substitution, however, liver Hg content stabilized at the end of 50 days and actually showed slight decreases during the next 50 days of feeding. At the 100% level of feeding, however, liver Hg increased continually during the entire feeding period, but the ratio of liver Hg to muscle Hg was slightly lower in this experiment and probably reflects the lower Hg content in the diet. These results confirm the observation made

TABLE 3. Mercury content of coho salmon (*Oncorhynchus kisutch*) livers fed OMP-type diets containing various quantities of dogfish meal (DF) (Expt 2).

Time	Diet			
Days and months	Control (*Hg-ppm*)	50% DF[a] (*Hg-ppm*)	75% DF[a] (*Hg-ppm*)	100% DF[a] (*Hg-ppm*)
0 (May)	0.07	0.07	0.07	0.07
30 (June)	0.10	0.12	0.16	0.21
60 (July)	0.06	0.15	0.19	0.24
90 (Aug.)	0.07	0.24	0.31	0.40
120 (Sept.)	0.07	0.24	0.32	0.46
150 (Oct.)	0.08	0.31	0.38	0.52
180 (Nov.)	0.07	0.26	0.35	0.56
210 (Dec.)	0.06	0.26	0.32	0.59

[a]Percent of dogfish meal substituted for herring meal.

in Expt 1 that although Hg rapidly accumulates in the liver it is not immobilized in this organ.

GROWTH

Expt 1 — Despite vaccination, all experimental lots and controls showed evidence of *Vibriosis* beginning late in the November–January period. The disease was determined to be a seriologically different strain of *V. anguillarum* than used in the vaccine (Harrell et al. 1976). The erratic occurrences of high mortalities were recorded from the onset of disease through the termination of the experiment in April 1974 so that statistical treatment of growth data was inapplicable in this experiment. A trend toward reduced growth in the experimental diets, however, was observed after 90 days (Fig. 3), and after 157 days a large reduction in the growth rate of the fish fed the experimental diets was evident. Apparently growth was further reduced in fish fed experimental diets containing 5% dehydrated orange peel and PG.

Expt 2 — Near the termination of the experiment (November–December), we found that otters had managed to enter the cages and had eaten some experimental fish from all lots. The populations were reduced to such an extent the statistical treatment for growth from this period on was not applied. Growth data is therefore presented only from April through November. Loss of fish also occurred from one of the control diet cages in September when fish escaped through a small hole in the net and data for this replicate are not presented following the escape.

A one-way analysis of variance was used to test for significant differences among fish weights for the three experimental lots containing dogfish

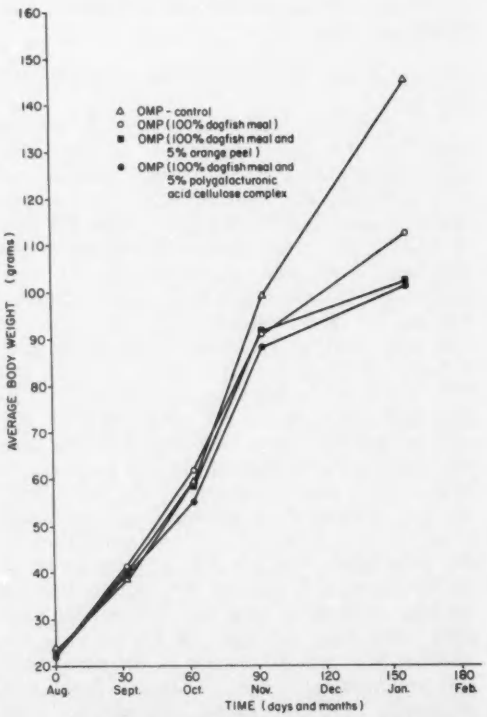

FIG. 3. Change in mean body weight of coho salmon fed OMP and OMP-type pellets in which 100% of the fish meal was substituted with dogfish meal. Effect of adding 5% dehydrated orange peel or 5% PG to these diets is also shown (Expt 1).

meal at the November 5 weighing period (control replicates excluded). Highly significant differences ($P < 0.001$) did occur. Using the mean square for the three dogfish diets as an estimate of the

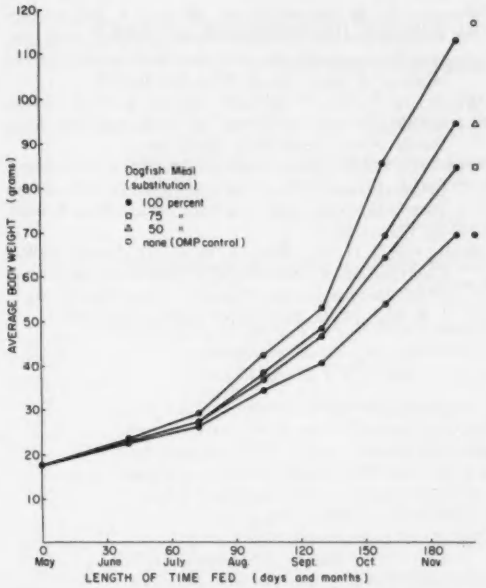

FIG. 4. Change in mean body weight of coho salmon fed OMP and OMP-type diets in which 50, 75, and 100% of the fish meal was replaced with dogfish meal (Expt 2).

variance of all lot means and applying Tukey's test (Snedecor 1956), it was found that significant differences ($P < 0.001$) did occur between all pairs of the eight lot means by November (including control replicates).

Because of experimental design Expt 1 and 2 cannot be directly compared; yet it does appear that after 60 days (Fig. 3 and 4) the growth of fish fed diets containing dogfish meal was retarded compared to those fed the OMP control diets. Results of the second experiment, however, show more definitive results: during a 157-day period there was 38, 27, and 18% reduction in weight gain between the OMP control diet and the experimental diets in which 100, 75, and 50% of the herring meal was, respectively, replaced with dogfish meal. Some evidence relating to the poor nutritional quality of the experimental diets was observed in Expt 2. Here we found that hematocrits ranged from 43 to 47% cell volume in the fish fed the experimental diets as compared to 54–55% cell volume in the fish fed on commercial OMP in other experiments during the same period.

Further evidence relating to the poor nutritional quality of dogfish as a component of salmonid diets was recently described by Satia and Brannon (1975). They reported that the growth of coho fry was adversely affected when fed diets containing high levels of dogfish as compared to coho fry fed diets containing other fish by-products and commercial OMP.

Acknowledgments

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Delayed Recruitment Models and Their Application to the American Lobster (*Homarus americanus*) Fishery

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A delayed recruitment model intended for use in developing dynamic strategies for fisheries management is proposed. The conceptual and analytical properties of the model are elaborated and compared with those of the instantaneous model of Schaefer and the delayed recruitment model recently suggested by Walter. Of the three models discussed, the delayed recruitment model proposed herein constitutes the more biologically meaningful tool for use in management decision making with fisheries characterized by a multiple year delay between spawning and recruitment. The proposed delay and Schaefer models are fitted to catch and effort data from the Rhode Island inshore pot lobster fishery, and the generated coefficients are examined with respect to their interpretation and relative importance. Values of optimum equilibrium catch and effort are calculated for the proposed delay and Schaefer models, and we show that the delay model's estimates of these management indices are more conservative than those derived from Schaefer's model. The proposed delay and Schaefer models are compared in a dynamic analysis of the fishery, in which perturbations in the stock level and fluctuations in the applied effort are simulated to predict the subsequent behavior of the stock.

MARCHESSEAULT, G. D., S. B. SAILA, AND W. J. PALM. 1976. Delayed recruitment models and their application to the American lobster (*Homarus americanus*) fishery. J. Fish. Res. Board Can. 33: 1779–1787.

Les auteurs proposent un modèle de recrutement retardé permettant de développer des stratégies dynamiques pour la gestion des pêches. Ils décrivent les propriétés conceptuelles et analytiques du modèle qu'ils comparent avec celles du modèle instantané de Schaefer et du modèle de recrutement retardé récemment proposé par Walter. Ils suggèrent que, parmi les trois modèles examinés, le modèle proposé est celui qui donne le meilleur fondement biologique aux décisions à prendre dans la gestion de pêches caractérisées par un décalage de plusieurs années entre la ponte et le recrutement. Les auteurs adaptent les modèles aux données de prise et d'effort de la pêcherie côtière de homard aux casiers du Rhode Island, et ils analysent les coefficients ainsi obtenus quant à leur interprétation et leur importance relative. Ils calculent les valeurs d'équilibre optimal entre la prise et l'effort pour le modèle à retardement proposé et le modèle instantané, et démontrent que les estimés de ces indices de gestion obtenus à l'aide du modèle à retardement sont plus conservateurs que ceux obtenus à l'aide du modèle de Schaefer. Ils comparent le modèle à retardement proposé et le modèle instantané dans une analyse de simulation dynamique de la pêcherie, dans laquelle les perturbations dans le niveau du stock et les fluctuations de l'effort appliqué sont simulées dans le but de prédire le comportement subséquent du stock.

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Two basic models of fisheries population dynamics and management have been widely applied. The first type of model is exemplified by the works of Beverton and Holt (1957) and Ricker (1975). This production type of model is expressely applicable to fisheries for which there are adequate data available regarding the elemental physiological rates of growth and natural mortality as well as recruitment and fishing mortality. The magnitudes and relationships of these rates are estimated from the available data, and

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they are combined in an appropriate form of the generalized model:

$$\frac{1}{P}\frac{dP}{dt} = r(P) + g(P) - M(P) - F(X) \pm n \quad (1)$$

where n is a variable due to external environmental factors. The coefficients r, g, and M express elemental rates of recruitment, growth, and natural mortality with respect to the population biomass P. The function F(X) expresses the loss of population biomass as a result of fishing mortality.

The alternative approach does not attempt to distinguish between recruitment, growth, and natural mortality, but considers only their resultant effect as a single function of the population size. This surplus yield approach to modeling has widespread application to fisheries which have not been exhaustively studied and for which growth rates are not easily obtained, but for which a need for regulation nevertheless exists. The approach stems from the logistic law of population growth and has been utilized and applied to the dynamics of a fishery by Schaefer (1954, 1957). The model is described as follows:

$$\frac{1}{P}\frac{dP}{dt} = f(P) - F(X) \quad (2)$$

The utility of this approach in population dynamics depends upon being able to apply a simple approximation to $f(P)$, the function describing population growth. Schaefer has assumed that $f(P)$ is linear with P.

Silliman (1971) recently reviewed the surplus–yield models and noted some of the shortcomings which are inherent in the approaches of Schaefer and others. Chief among these is the assumption that the time lag between spawning and recruitment is of little consequence with respect to population growth. Schaefer (1957) and Schaefer and Beverton (1963) clearly acknowledge the shortcomings by outlining the above assumption and the assumption that the rate of natural increase at a given weight of population is independent of the age structure of the population.

A number of attempts have been made to include time lag parameters in population dynamics models to eliminate the assumption of no delay between spawning and recruitment. Time lag models are essentially of two types: discrete lag and continuous lag models. In the discrete lag formulation, the rate of population change depends, in the simplest case, on the population size at two discrete points in time, (t) and $(t - \omega)$. For example, if a population is characterized by a delay of (ω) years between spawning and recruitment, then it follows that the current growth in the populaiton will be a function of the population level (ω) years ago.

Continuous lag models, however, reflect the current rate of population change as a function of an infinite number of values of P over the interval from $(t - \omega)$ to (t). Here the current rate of population change is not simply a function of the population (ω) years ago, but is dependent also upon the dynamics of the population since spawning.

Recently Caswell (1972) utilized the continuous lag approach in a modification of the Volterra–Gause equations. Much of the significant work with discrete lag models has been done by Leslie (1959), who used matrix-difference equations, and Wangersky and Cunningham (1957), who used differential-difference equations. The discrete lag approach to modeling is particularly amenable to analyzing the impact of the lag between spawning and recruitment on population dynamics in that one or more events in the life history of the species may be readily considered.

The objectives of this study are twofold. Firstly, a proposed delayed recruitment model is developed and compared with the Schaefer model and with an existing delayed recruitment fishery model. Secondly, the models are applied to a management analysis of the population dynamics of the Rhode Island inshore lobster fishery.

Theory and Analysis of Delayed Recruitment Models Intended for Fishery Management

Application of delay terms to models intended for fishery management was recently discussed by Walter (1973). Noting the basic shortcomings of the surplus–yield approach to fishery management, Walter offered a formulation which overcomes the problem of time delayed recruitment on population growth, while maintaining the basic data requirements of only catch and effort statistics. The equations proposed by Walter have the same form as the Schaefer model, except that one or more terms involving the population a number of years previously are included.

Walter has taken the generalized form of the logistic model,

$$\frac{1}{P}\frac{dP}{dt} = b - aP \quad (3)$$

and expanded it to assume the form:

$$\frac{1}{P}\frac{dP}{dt} = b - a_1P(t) + a_2P(t - \omega) \quad (4)$$

where (ω) is the time lag between spawning and recruitment. In the latter equation the coefficients b, a_1, and a_2 are the coefficients of instantaneous growth, density dependence, and recruitment, respectively. The introduction of fishing pressure has the effect of changing the coefficient b and lowering the equilibrium level. This term is included as:

$$\frac{1}{\mathrm{P}}\frac{d\mathrm{P}}{dt} = b - a_1\mathrm{P}(t) + a_2\mathrm{P}(t-\omega) - qf(t) \quad (5)$$

where $f(t)$ is applied fishing effort and q is the coefficient catchability.

The model as presented above suggests that the current rate of population growth depends in part upon the population level at a single previous time, when in fact it may depend upon the population at a number of previous times. As Walter points out, this may also be the case when (ω) is unknown or at least cannot be chosen accurately. To account for this, additional delay terms may be added as:

$$\frac{1}{\mathrm{P}}\frac{d\mathrm{P}}{dt} = b - a_1\mathrm{P}(t) + a_2\mathrm{P}(t-\omega) + a_3\mathrm{P}(t-2\omega) \ldots + a_{n+1}\mathrm{P}(t-n\omega) - qf(t) \quad (6)$$

An alternative approach to the problem of incorporating delay parameters into fisheries management models is now proposed. The formulation consists of an expansion of the generalized Schaefer model, but differs structurally and conceptually from that of Walter. This model, in the presence of fishing pressure assumes the form:

$$\frac{d\mathrm{P}}{dt} = b\mathrm{P}(t) - a_1\mathrm{P}(t)^2 + a_2\mathrm{P}\,t-\omega) - qf(t)\mathrm{P}(t) \quad (7)$$

in which the time delay term is independent of the current population level.

The structure of the proposed delay model states that the rate of change of the population is a function of the current population level and fishing effort, as well as recruitment from some past spawning population. Moreover, the model implies that recruitment is effectively independent of the present population biomass. This interpretation differs from that implied by the Walter model, which we interpret as implying that the rate of recruitment is directly proportional to the product of the current and spawning population levels. The suggested relationship does not appear tenable, regardless of population density considerations. If a relationship between recruitment and the size of the current population exists, it seems that the rate of recruitment would be slowed by some density dependent mechanism such as cannibalism or competition for food. If this were the case, one would expect an inverse relationship between the number of recruits entering the fishery and the magnitude of the current stock. This latter interaction is not consistent with the functional relationship for recruitment expressed in the Walter model.

We suggest that due to the difficulty in quantifying the functional relationships between current and spawning populations, it may be sufficient, as well as biologically reasonable, to present the rate of recruitment as being dependent only on the spawning population level. Additional discussion of this point will be presented in a forthcoming formal mathematical analysis of delayed recruitment models which are similar in form to those discussed here.

The above models can be used in an analysis of optimum population levels, optimum levels of applied fishing effort, and maximum equilibrium yield. From the Schaefer model,

$$\frac{d\mathrm{P}}{dt} = b\mathrm{P} - a\mathrm{P}^2 - qf\mathrm{P} \quad (8)$$

it follows directly that the optimum equilibrium population level, $\mathrm{P}_o{}^*$, may be derived by finding that equilibrium value of the population for which the equilibrium yield ($qf_o\mathrm{P}_o$) is a maximum:

$$\mathrm{P}_o{}^* = \frac{b}{2a} \quad (9)$$

Similarly the optimum equilibrium fishing effort corresponding to $\mathrm{P}_o{}^*$ is

$$f_o{}^* = \frac{b}{2q} \quad (10)$$

which leads to an expression for maximum equilibrium yield:

$$\mathrm{Y}_o{}^* = qf_o{}^*\mathrm{P}_o{}^* = \frac{b^2}{4a} \quad (11)$$

Applying this analysis to the proposed delay model and noting that in equilibrium $\mathrm{P}(t)$ is equal to $\mathrm{P}(t-\omega)$, it follows that for the proposed delay model:

$$0 = (b + a_2)\mathrm{P}_o - a_1\mathrm{P}_o{}^2 - qf_o\mathrm{P}_o \quad (12)$$

From equation (12) it can be shown that expressions for the optimum equilibrium population level, the optimum equilibrium fishing effort, and the maximum equilibrium yield for the proposed model, are, respectively:

$$\begin{aligned} &\text{i)} \quad P_o^* = (b + a_2)/2a_1 \\ &\text{ii)} \quad f_o^* = (b + a_2)/2q \\ &\text{iii)} \quad Y_o^* = (b + a_2)^2/4a_1 \end{aligned} \tag{13}$$

The validity of such a modeling approach as that of Schaefer is that where reasonable population estimates are not available, catch and applied effort statistics may be used to reflect the dynamics of the fishery. In this case the catch-per-unit effort statistic is assumed to be proportional to the biomass of the entire population to which the effort is applied, and hence, is a biologically reasonable indicator of the behavior of the population. The models assume that catch Y is equal to qfP, and hence that catch-per-unit-effort, N, is equal to qP. From the latter expression it follows that the Schaefer model (equation 8) may be equivalently expressed as:

$$\frac{dN}{dt} = bN - a_{12}N^2 = qfN \tag{14}$$

where a_{12} equals $\frac{a}{q}$ from equation (8)

This form of the model enables one to draw inferences about the magnitude of the exploited population from catch-per-unit-effort (CPUE) data. From equation (14) it follows that when catch-per-unit-effort (CPUE) data is used in lieu of population biomass data, the optimum equilibrium population level and maximum equilibrium yield can be rewritten for the Schaefer model as,

$$\begin{aligned} &\text{i)} \quad Y_o^* = b^2/4a_{12}q \\ &\text{ii)} \quad P_o^* = b/2a_{12}q \end{aligned} \tag{15}$$

and the expression for optimum equilibrium fishing effort remains unchanged. The proposed delay model (equation 7) may be expressed in terms of CPUE as:

$$\frac{dN}{dt} = bN(t) - a_{12}N(t)^2 + a_2N(t - \omega) - qf(t)N(t) \tag{16}$$

where $a_{12} = \frac{a_1}{q}$ from equation (7).

From the generalized form of the Schaefer model (equation 8) and the equilibrium population value P_o, it is possible to derive an expression for yield with respect to applied effort:

$$Y_o = \frac{qf_o}{a}(b - qf_o) \tag{17}$$

Under the assumption that at equilibrium $P(t)$ is equal to $P(t - \omega)$, equation (17) may be extended to the delay model. For the proposed delay model it can be shown that the expression for yield in terms of applied effort assumes the form:

$$Y_o = \frac{qf_o}{a_1}(b + a_2 - qf_o) \tag{18}$$

The problem of fitting the Schaefer (instantaneous) and proposed delay models to available catch and effort data was approached on the basis of simplicity and precedent. The method selected for this process was multiple linear regression. While there may be some question as to the applicability of multiple regression, based upon the assumed independence of the variables, the method has been developed for the analysis of delayed recruitment models (Walter and Hogman 1971) and represents an acceptable first approach to the analysis at hand. The approach consists of approximating the relative derivative, $\frac{1}{N}\frac{dN}{dt}$, as

$$\frac{1}{N}\frac{dN}{dt} = 2\frac{N(i + 1) - N(i)}{N(i + 1) + N(i)} \tag{19}$$

where $N(i)$ is the mean catch-per-unit-effort in a given year (i), and $N(i + 1)$ is that value 1 yr later. In this case $1/N$ is taken as the average value of the population biomass over the year of growth. This averaging procedure tends to reduce the derivative calculation's sensitivity to noise in the data. This approximation is considered to be best when data are available on a yearly basis (Walter and Hogman 1971). The variables on the right side of the model equation are then given their exact yearly values.

Multiple regression techniques are applied to the data to generate values for the coefficients b, a_{12}, a_2, and q, which in turn give the least squares approximation to the relative derivatives calculated above. A considerable amount of care should be taken at this point to evaluate the coefficients in terms of their biological interpretation. The signs of the coefficients are of interest in fisheries models. For biological reality we require the signs to reflect the positive contribution of growth and recruitment, as well as the negative effect of fishing mortality and density dependence on the overall dynamics of the population.

The coefficients of the models are of particular interest when the above formulae for optimum equilibrium population level, optimum equilibrium effort, and maximum equilibrium yield are used for management decisions. Additionally, the re-

sponse of the population to random perturbations in the population level or changes in the applied effort may prove to be a critical consideration in the management strategy. Clearly it would be beneficial to have a feeling for the rate of recovery of a population, whose level had been supressed for some reason, before equilibrium fishing effort could be resumed.

Because the Schaefer and proposed delay models respond differently to perturbation, it becomes necessary to simulate the models to observe their dynamic behavior. For the purposes of this report, simulations involve a numerical solution to the differential equations using the Euler method. Initially a simulation is described using the initial conditions for the time series of data involved to give an indication of the accuracy with which the series data can be reproduced based upon the approximation of the differential equation by a difference equation. Additionally, simulations are described which incorporate equilibrium values for initial conditions, and in which perturbations are introduced to observe the response characteristics of the models.

The Rhode Island Inshore Lobster Fishery

The application of a management model which considers recruitment as a fundamental contributor to population growth and dynamics is of particular interest with respect to the American lobster (*Homarus americanus*). Examination of the relationship between lobster stock and recruitment reveals that under present conditions of heavy exploitation, annual recruitment contributes substantially to the size of the fishery. In the Rhode Island inshore pot lobster fishery, current legal restrictions prohibit taking lobsters shorter than 78-mm carapace length. Moreover, current fishing pressure exerted on the lobster population is sufficiently high such that the majority of the catch is at the legal limit. Empirical laboratory growth data of Hughes and Matthiessen (1962) suggest that the catchable size may be achieved in about 5 yr, thus corresponding to a similar time delay between spawning and recruitment.

Thus, any management strategy attempting to impose regulatory restrictions upon the lobster fishery must consider recruitment. Hancock (1973) has observed that in the European lobster (*H. vulgaris*) there is no empirical evidence of a correlation between the numbers of adults and the numbers of recruits entering the fishery. He does not, however, indicate whether appropriate delays were considered, nor the extent of the data examined. As such, observations of this nature should not be taken as definitive evidence for not assuming a basic relationship between spawners and recruits. In a simulation study of sex ratios and regulation effects with *H. americanus*, Saila and Flowers (1965) have demonstrated that the protection of berried females (as is the case in Rhode Island) resulted in stable sex ratios near unity. The latter tends to support the assumption of a proportional relationship between recruitment and some spawning population, as expressed in the proposed model.

Many parameters may influence the stock–recruitment relationship for lobster. Environmental variability, particularly fluctuations in temperature, has been shown to be correlated with the magnitude of the annual recruitment (Flowers and Saila 1972). Additionally, density dependent effects which may reflect crowding or resource limitation can be assumed operative in prerecruit populations. The proposed delay model attempts to account for the high dependence of yield upon annual recruitment in the lobster fishery, while operating within the framework of an already established management model. Accounting for recruitment in terms of a linear function of the spawning population falls somewhat short of defining the functional relationships actually operative in the lobster fishery, considering the demonstrated dependence upon temperature fluctuations. The raison d'être for the model, however, is to provide a management tool which may be easily applied, utilizing available data. While the effect of temperature fluctuations should not be ignored in a more exact, species-specific model, data for temperature distributions and physiological interactions are not readily available. Moreover, the inclusion of environmental terms into the model proposed would compromise its general applicability in management decision making.

Catch and effort statistics for the Rhode Island inshore pot lobster fishery are presented in Table 1 for the period 1930–67 (Anon. 1930–67). To fit regression models to these data, the relative derivative was approximated as in equation (19) and time delays of $\omega = 4$, 5, and 6 yr were considered. A value of $\omega = 5$ provided the best fit for the proposed delay model.

A single delay term was considered in this application for two reasons: firstly, in the heavily exploited lobster fishery, sexual maturity coincides closely with age at recruitment, and the greatest contribution to total fecundity comes from this group; secondly, additional delay terms may provide for unwarranted complexity in the model for the general case, and certainly for this application.

TABLE 1. Catch, effort, and catch-per-unit-of-effort for the Rhode Island inshore lobster fishery, 1930–67. Data obtained from Rhode Island landings.

	Catch ($lb \times 10^3$)	Effort ($pots \times 10^3$)	Catch/unit effort (lb/pot)	$\frac{1}{N}\frac{dN}{dt}$
1930	1353.0	39.2	34.5	—
1931	1259.2	40.8	30.8	—
1932	1257.2	42.1	29.8	—
1933	708.1	53.6	13.2	—
1934	—	—	—	—
1935	618.9	25.3	24.5	.036
1936	693.4	27.3	25.4	.038
1937	773.7	29.3	26.4	−.078
1938	709.4	29.0	24.4	.020
1939	635.8	25.5	24.9	−.587
1940	272.6	20.1	13.6	.591
1941	390.0	16.0	25.0	.402
1942	432.7	11.5	37.6	−.361
1943	292.4	11.2	26.1	−.211
1944	234.2	11.1	21.1	.212
1945	266.7	10.2	26.1	−.035
1946	359.8	14.3	25.2	.050
1947	392.7	14.8	26.5	−.066
1948	382.7	15.4	24.8	−.195
1949	354.6	17.4	20.4	−.087
1950	250.0	13.4	18.7	.244
1951	211.1	8.8	23.9	−.187
1952	91.2	4.6	19.8	.092
1953	121.4	5.6	21.7	.092
1954	190.4	8.0	23.8	.162
1955	221.5	7.9	28.0	−.137
1956	200.3	8.2	24.4	.416
1957	260.7	7.0	37.2	−.156
1958	299.5	9.4	31.8	.043
1959	408.1	12.3	33.2	.252
1960	454.4	10.6	42.8	−.050
1961	387.2	9.5	40.7	−.133
1962	259.8	7.3	35.6	−.485
1963	167.6	7.7	21.7	.271
1964	199.7	7.0	28.5	.443
1965	380.6	8.5	44.7	−.036
1966	508.5	11.8	43.1	−.108
1967	511.0	13.2	38.7	—

TABLE 2. Model coefficients (MC), multiple correlation coefficients (MCC), and standard errors of estimate (SE) for regression models corresponding to the Schaefer instantaneous model and the proposed delay model.

Conceptual model for regression	MC	MCC	SE
$\frac{1}{N}\dot{N} = b + a_{12}N + qf$ (Schaefer)	$b = .5489$ $a_{12} = -.0153$ $q = -.0081$	.460	.238
$\frac{1}{N}\dot{N} = b + a_{12}N(t) + a_2\frac{N(t-\omega)}{N(t)} + qf$ (Proposed delay)	$b = .0492$ $a_{12} = -.0085$ $a_2 = .2983$ $q = -.0068$	.544	.229

TABLE 3. Predicted values of optimum equilibrium population, optimum equilibrium applied effort, maximum equilibrium yield, and optimum equilibrium CPUE for the Rhode Island inshore lobster fishery.

Model	P_o^* (*klb*)	f_o^* (*kpots*)	Y_o^* (*klb*)	N_o^* (*lb landed/pot*)
Instantaneous (Schaefer)	2226.8	34.01	610.9	17.97
Proposed delay	3007.3	25.47	522.0	20.51

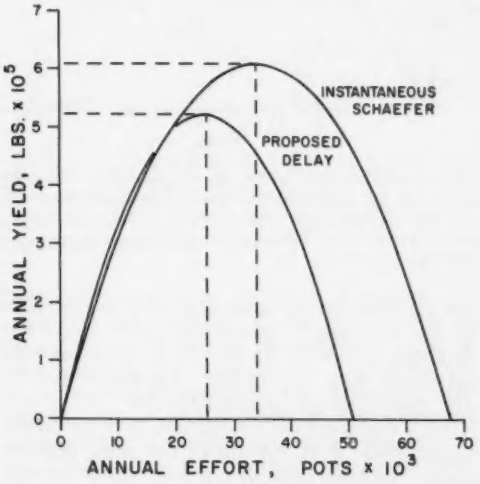

FIG. 1. Predicted values of annual yield with annual effort for the Rhode Island inshore lobster fishery given by the proposed delay and instantaneous Schaefer models.

The regression coefficients generated for the models are listed in Table 2, and it is clear that all are conceptually acceptable with respect to sign. With regard to the multiple correlation coefficients and error statistics generated for the regressions, the proposed delay formulation accounts for more of the variability in the data and reduction in the standard error of estimate than does the Schaefer model. The improvement in accounting for variability shown by the delay model is significant at the 0.07 level.

It is recognized that recruits to the lobster fishery are cropped quite soon after entry, and as such are expected to contribute the most to annual yield. Regression coefficients (Table 2) for the delay model give a clear indication of the relative importance which this model places upon growth within the population and annual recruitment with respect to yield. The Schaefer model doesn't distinguish growth due to recruitment and considers instantaneous growth from within the catchable stock to be responsible for total yield. As such, the Schaefer model cannot be expected to be dynamically responsive to the intrinsic behavior of this fishery.

The validity of the proposed delay model has been supported both on the basis of its conceptual design and with respect to its application to the lobster fishery. We suggest that the model represents a suitable and meaningful application of time delayed recruitment to the management of the lobster fishery. Remaining to be discussed are the predictive characteristics and the implied management strategies of the proposed delay model. These will be considered in relation to the Schaefer (instantaneous) model; the latter being established and widely used in formulating management decisions.

Based upon the management indices generated for the proposed delay and instantaneous models (Table 3), it is clear that different management strategies are projected. Primarily, the instantaneous model predicts that over 27% of the calculated equilibrium population can be cropped annually, which contrasts with the 17% predicted by the proposed model. The conservative nature of the yield prediction of the proposed model leads to a similar management strategy in which it is suggested that yields in excess of the predicted optimum equilibrium may result in a condition of overfishing. Additionally, while the yield prediction of the delay model is 14.5% lower than that predicted by the instantaneous model, the prediction of optimum equilibrium effort for the proposed model is 25% less, resulting in the prediction of an overall higher catch for each unit of applied effort by the proposed model. The relationship between yield and effort, based upon the coefficients of the instantaneous and proposed delay models (equations 17, 18), is illustrated in Fig. 1. Although the optimum equilibrium effort and yield predictions of the proposed model depend heavily upon the level of the spawning population some years earlier and tend to be insensitive to specific environmental variations prior to recruitment, we believe that the fishery manager is supplied with a reasonable set of indices which will permit the implementation of an adequate management strategy.

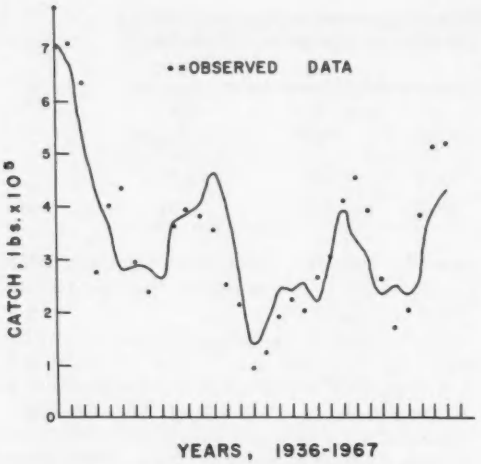

FIG. 2. Values of catch predicted by the proposed delay model with annual catch data for the Rhode Island inshore lobster fishery (1936–67).

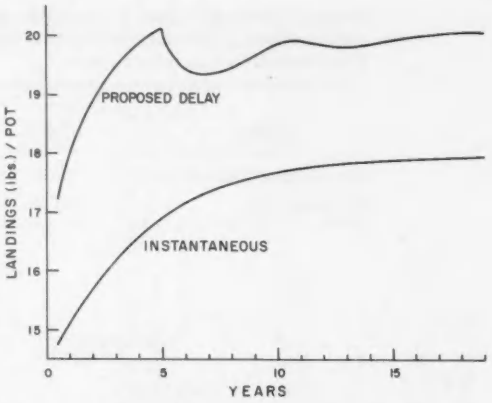

FIG. 3. Predicted values of CPUE (N) with time given by the proposed delay and instantaneous models. Initial conditions: $N(t_o) = .8 \times$ the appropriate equilibrium value; fishing effort held constant at equilibrium (see Table 3).

The management implications discussed to this point are based upon equilibrium analysis of model coefficients and as such do not consider the dynamic aspects of the model which must influence management decision making. Discussion of the dynamics of the models will include predicted behavior under conditions of stress and perturbation. Simulation of the models will involve the numerical solution of the differential equations via the Euler method in which a step size of 0.1 was found to be adequate.

Initially, the delay model is simulated with respect to the initial conditions established by the 1st 6 yr of data (Table 1). The simulation is designed to give an indication of the error associated with approximating the explicitly defined differential equation by a difference equation in which the data are considered in increments of 1 yr. Values of catch predicted by the delay model for the period 1937–67 were correlated with actual values for those years. The correlation coefficient calculated for the delay model was $r = 0.89$, which is interpreted to indicate that the difference equation approximation is reasonable. Predicted and actual values of yearly catch for the simulation period are shown in Fig. 2.

Behavior of the lobster stock predicted by the proposed delay and instantaneous models with respect to a perturbation in the current stock level is shown in Fig. 3. The stock (measured as CPUE) is taken to have been in equilibrium for 5 yr and the initial conditons of the simulation reflect the instantaneous perturbation. Specifically the perturbation constitutes a reduction of 20% in the appropriate equilibrium stock level. The dynamics predicted by the proposed model are consistent with recruitment dependent growth. The rapid increase through the 1st 5 yr clearly reflects augmentation by recruits from spawning stocks. After 5 yr, growth of the stock depends upon a variable input of recruits relative to non-equilibrium spawning population levels. The stock level predicted by the instantaneous model increased in a monotonic fashion, attaining equilibrium before that predicted by the proposed model. Clearly management decisions designed for the regulation of the lobster stock must consider the oscillatory behavior in the trend of the stock relative to equilibrium over time, as well as the amount of time required for the stock to respond in general.

Assuming that the lobster stock is initially in equilibrium, it is possible to simulate the effects of altering the applied fishing pressure. The relative sensitivity of the stock to overfishing (Fig. 4) is explored through simulating a 50% increase in applied effort. At the end of 5 yr of simulation the delay model predicts that the stock has dropped about 15%, whereas the instantaneous model predicts a 35% decay. The dependence of the proposed model upon delayed recruitment has acted to diminish the predicted consequences of overfishing. A management strategy formulated with respect to the delay model's predictions would necessarily involve a much more moderate regulation of the applied effort required to restore the stock to its equilibrium level.

Simulations involving conditions of overfishing

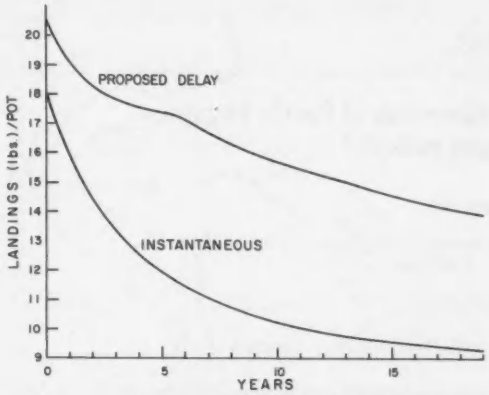

FIG. 4. Predicted values of CPUE (N) with time given by the proposed delay and instantaneous models. Initial conditions: $N(t_o)$ = the appropriate equilibrium value; fishing effort held constant at 1.5 × the equilibrium value (see Table 3).

and underfishing with the delay model demonstrate that the stock is not critically sensitive to these factors. Overfishing the catchable stock by some finite level does not diminish the potential of the prerecruit populations for augmenting subsequent annual yields. Although the catchable stock will decay, the rate will be less drastic than that predicted by the instantaneous model. Possibly the most important factor illustrated by the delay model for management decision making is the amount of time available for analyzing the impact of applied strategies and making appropriate adjustments. Use of the Schaefer model as a management tool would require that strategies be implemented which were inappropriate to the actual condition of the stock. Additionally, any decision would have to be made within a shorter time frame, allowing for the possibility of increased error. Simulations of the type mentioned here use equilibrium values as initial conditions such that the dynamic predictions of the model are in response to the stress being tested without the additional influence of an already nonequilibrium stock level. While other simulation schemes may provide additional insight into the dynamics of the lobster fishery with resultant management implications, we believe that those described will suffice in the interest of brevity. Prediction of future trends in the lobster fishery would require that some effort strategy be assumed, and management strategies cannot be explored within the scope of this study.

Acknowledgments

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Sperm Density During Active Spawning of Pacific Herring (*Clupea harengus pallasi*)[1]

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HOURSTON, A. S., AND H. ROSENTHAL. 1976. Sperm density during active spawning of Pacific herring (*Clupea harengus pallasi*). J. Fish. Res. Board Can. 33: 1788–1790.

Discharge of milt by spawning Pacific herring (*Clupea harengus pallasi*) produces a milky discoloration in the water which is readily observed under favorable conditions of weather and light. Echo-sounder tracings showed that only the inshore part of a spawning school that was in contact with the bottom participated in the early stages of spawning. Sperm densities at the surface for two spawnings averaged 148 and 129 sperm/ml (range 80–210 for 16 subsamples). This density is considered more than ample for high fertilization success but is only one-tenth that normally used for artificial fertilization in the laboratory at Nanaimo.

HOURSTON, A. S., AND H. ROSENTHAL. 1976. Sperm density during active spawning of Pacific herring (*Clupea harengus pallasi*). J. Fish. Res. Board Can. 33: 1788–1790.

L'émission de laitance par le hareng du Pacifique (*Clupea harengus pallasi*) en voie de fraie produit une décoloration laiteuse de l'eau facilement observable quand les conditions de température et de lumière sont favorables. Des enregistrements de sondeur à écho démontrent que seule la portion côtière d'un banc reproducteur en contact avec le fond participe aux premières phases de la fraie. La densité des spermatozoïdes à la surface lors de deux pontes était en moyenne de 148 et de 129 spermatozoïdes/ml (extrêmes de 80 à 210 dans 16 sous-échantillons). Nous considérons cette densité comme étant plus qu'amplement suffisante pour assurer un haut degré de fécondation, mais elle n'est qu'un dixième de celle normalement utilisée pour la fécondation artificielle en laboratoire à Nanaïmo.

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ALTHOUGH Pacific herring (*Clupea harengus pallasi*) spawnings in British Columbia waters usually produce a highly visible milky discoloration in the water at their peak (Outram and Humphreys 1974), opportunities for photography and sampling are limited. Exact timing and location of spawnings vary from year to year (Outram and Haegele [1969] and previous reports in that series, and Humphreys and Webb [1970] and subsequent reports in that series). Since peak spawning usually occurs within 3 or 4 h of the initial discoloration of the water, the area that can be monitored effectively is limited. Moreover, much of the spawning occurs under poor weather conditions or in the long hours of darkness which prevail during the winter and would be difficult to detect visually in time to sample sperm densities.

In 1975, however, a fortuitous series of circumstances occurred. For the first time in over 25 yr, major herring spawnings occurred within sight of the Pacific Biological Station. Some of these took place in daylight under ideal weather conditions. Two such spawnings were examined by echo sounder and surface water samples were collected for sperm density determinations.

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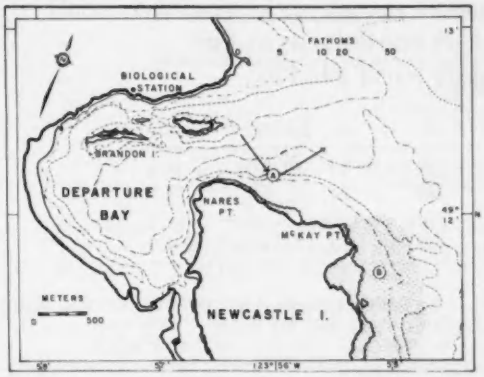

FIG. 1. Sampling locations (A and B) and sounder track (arrows to and from Station A). Depths in meters.

Materials and methods — On March 24, 1975, a milky discoloration of the water became visible at about 1100 along the northern shore of Newcastle Island. At the height of discoloration (1400) when the milky patch extended for about 750 m along the shore and up to 1000 m offshore, covering about 400,000 m², a bucket of water was drawn from the surface within the area of maximum discoloration (Station A, Fig. 1). Two samples were taken from the bucket for sperm density determinations. In addition, a water sample was taken to determine salinity. By 1600 disintegration of the milky patch was well under way.

About the same time, a second spawning 3.2 km long occurred along the east coast of Newcastle Island. Here the water was discolored to about the same extent for an average of about 500 m from the shore. A second pair of samples was taken from this spawning at Station B (Fig. 1).

Four subsamples were taken from each of the four samples collected, and sperm counts were made in a Neŭbaŭr cell within 2 h after collection.

Schools involved in both spawnings were observed on a Simrad EM 2F 38kHz sounder.

Results and discussion — Echo-sounder records at the time of spawning show a school of herring extending offshore for a distance of approximately 700 m at a depth of 6–18 m. The center of milt concentration, as indicated by milky discoloration of the water, was over the point where the school contacted the bottom (Fig. 2). This is consistent with observations that spawning behavior involves contact by the female with a suitable substrate (Hourston et al. 1975). The record also shows that only part of the observed school was actively spawning at that time as the school extended well beyond the area of milt-discolored water in some places. The observed spawnings took place during the latter part of a

FIG. 2. Sounder track to and from Station A. Depths in meters.

rising tide (2.8 m at 0914 rising to 4.0 m at 1425) which is also consistent with other field observations of herring spawnings (R. D. Humphreys personal communication).

Records from a continuous surface temperature monitoring station on the north shore of Brandon Island (Fig. 1) approximately 2000 m from the first spawning, are considered representative of the waters in the area of spawning. On March 24, 1975, these records show that the temperature rose from 6.5 C at 1100 (when spawning began) to 8.7 C at 1500 and had declined to 8.0 C by 1600. The salinity sample taken during spawning showed 28.16‰. Both temperature and salinity were within the normal range for successful spawning in this area (6.5–9.0 C and 22.4–28.7‰, respectively — Outram [1975]). Therefore, this spawning would appear to be typical for British Columbia waters.

Sperm samples were taken at the apparent peak of spawning when the milky discoloration of the water was greatest. This was probably the peak period of fertilization as impregnation of the eggs is most successful between ½ h and 2½ h after release of both sperm and eggs (D. F. Alderdice personal communication). Sperm density varied between 80 and 210 sperm/ml (Table 1). Differences between sample means were less than 7% for both spawnings. Average sperm density in the area of maximum discoloration of the surface water was strikingly similar for the two spawnings (148 and 129 sperm/ml). These results provide a realistic estimate of sperm concentration at the surface under conditions of minimal dispersal (slack tide, negligible wind, sheltered waters). Sperm concentrations near the bottom, where eggs and sperm are released, should be somewhat higher.

Concurrent studies by H. Rosenthal showed that herring sperm are chemically attracted to the surface of the egg from a distance of at least 0.1 mm. Assuming that eggs are deposited in a single continuous layer so that 50% of the surface is exposed to the milt-laden water and that the eggs average 1 mm in diam (Outram 1955), the exposed area per egg would be 1.6 mm². Under these conditions, each egg would attract

TABLE 1. Density of Pacific herring (*Clupea harengus pallasi*) sperm (number per milliliter).

Stn.	Sample	Subsamples 1	2	3	4	Mean	SE
A	1	90	210	140	90	133	24.6
	2	120	120	180	80	125	17.8
B	3	140	150	110	210	153	18.2
	4	150	130	140	150	143	4.1

sperm from 0.16 ml of water, or 24 sperm when sperm density is 150/ml. Since fertilization success is close to 100% in natural spawnings involving more than one layer of eggs, a sperm density such as that observed at the surface for these two spawnings is apparently more than ample for high fertilization success.

Sperm densities used in rearing experiments at the Pacific Biological Station in 1974 and 1975 approximated 1500/ml — 10 times greater than those recorded above. Consequently, the reduced fertilization rates obtained in some of these experiments (Rosenthal 1968) cannot be attributed to insufficient density of the sperm.

These results may also have some implications for population studies. The relative uniformity of sperm density suggested by the above observations and the sharp boundaries of the milky water observed during spawning suggest the possibility of using sperm density and volume of discolored water to estimate the numbers of spawners. This would provide a much less laborious alternative to the present procedure of measuring the area and density of egg depositions (Hourston et al. 1972).

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Relative Effect of Two Dietary Water-Soluble Analogues of Menaquinone on Coagulation and Packed Cell Volume of Blood of Lake Trout (*Salvelinus namaycush*)

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POSTON, H. A. 1976. Relative effect of two dietary water-soluble analogues of menaquinone on coagulation and packed cell volume of blood of lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33: 1791–1793.

Triplicate lots of fingerling lake trout (*Salvelinus namaycush*) (initial mean weight, 5.3 g) were fed a basal, semipurified diet, or this basal diet supplemented with either 1.0 or 2.0 ppm of either menadione sodium bisulfite (MSB) or menadione dimethylpyrimidinol bisulfite (MPB) for 18 wk at 14 C. Neither form of vitamin K had a significant effect on the growth, food conversion, or body composition of the fish.

Fish fed 1 ppm of MSB had a significantly higher mean packed cell volume (PCV) than those fed 2 ppm of either analogue. Trout fed 2 ppm of MPB had an intermediate PCV which was not significantly different from that of trout fed either 1 ppm MPB or 2 ppm MSB. A dietary level of 1 ppm MPB (providing an equivalent menaquinone concentration of about 0.5 mg/kg of diet) is sufficient to insure normal coagulation of lake trout blood and a satisfactory PCV.

POSTON, H. A. 1976. Relative effect of two dietary water-soluble analogues of menaquinone on coagulation and packed cell volume of blood of lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33: 1791–1793.

Nous avons nourri des groupes en triplicata de fingerlings de touladi (*Salvelinus namaycush*) (poids moyen initial de 5.3 g) à un régime semi-purifié basal, ou à ce régime de base auquel on a ajouté 1.0 ou 2.0 ppm de bisulfite sodique de ménadione (MSB) ou de bisulfite diméthyl-pyrimidinol de ménadione (MPB) pendant 18 semaines à 14 C. Ni l'une ni l'autre forme de vitamine K n'ont d'effet significatif sur la coissance, la conversion des aliments ou la composition du corps des poissons.

Les poissons nourris à 1 ppm de MSB ont un volume moyen de cellules concentrées (PCV) nettement plus élevé que les poissons nourris à 2 ppm de l'un ou l'autre des analogues. Les touladis nourris à 2 ppm de MPB ont un PCV intermédiaire qui n'est pas très différent de celui des touladis nourris soit à 1 ppm de MPB soit à 2 ppm de MSB. Un niveau alimentaire de 1 ppm de MPB (donnant une concentration de ménaquinone équivalente d'environ 0.5 mg/kg de régime) suffit à assurer une coagulation normale du sang des touladis de même qu'un PCV satisfaisant.

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DIETARY 2-methyl-3-phytyl-1, 4-naphthoquinone (vitamin K_1) has been shown to reduce the whole blood clotting time and to elevate the packed cell volume (PCV) of brook trout, *Salvelinus fontinalis*, fed a semipurified diet (Poston 1964). Dietary 2-methyl-1, 4-naphthoquinone (menaquinone or vitamin K_3; also known commercially as menadione) prevented hemorrhage and death in channel catfish, *Ictalurus punctatus* (Dupree 1966) and anemia in rainbow trout, *Salmo gairdneri* (Kitamura et al. 1967).

In recent years manufacturers of animal feeds have predominantly used synthetic, water-soluble derivatives of vitamin K (Scott 1972). Several workers have compared the vitamin K activity of water-soluble analogues of menaquinone, including menadione sodium bisulfite (MSB) and menadione dimethylpyrimidinol bisulfite (MPB) in chicks (Frost et al. 1956; Nelson and Norris 1960; Dua and Day 1966; Griminger 1965). In general, MPB has been found to be the most active and stable in hastening blood clotting in the animals tested.

Although MPB has been approved as an additive in poultry and swine feeds in the USA (Fine 1975), little information is available on the relative effectiveness of MPB and MSB as sources of vitamin K in fish diets.

The present study was designed to compare the effect of two dietary levels of supplemental MPB and MSB in reducing clotting time and elevating percentage packed cell volume (PCV) of whole blood of fingerling lake trout, *Salvelinus namaycush* fed a semipurified diet.

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TABLE 1. Composition of basal diet fed to fingerling lake trout, *Salvelinus namaycush*.

Ingredient	Percent
Casein, vitamin-free	40
Gelatin	10
Soy oil	10
Sucrose	10
Dextrin	10
Cellulose	12
Minerals[a]	6.9
Vitamins[b]	0.9
L-Tryptophan	0.04
DL-Methionine	0.20

[a]Provided the following in grams per kilogram of diet: $CaHPO_4 \cdot 2H_2O$, 18.04; $CaCO_3$, 19.04; KH_2PO_4, 14.03; $NaHCO_3$, 8.82; NaCl, 5.0; $MnSO_4 \cdot H_2O$, 0.35; $FeSO_4 \cdot 7H_2O$, 0.50; $MgSO_4$, 3.02; KIO_3, 0.01; $CuSO_4 \cdot 5H_2O$, 0.03; $ZnCo_3$, 0.15; $CoCl_2 \cdot 6H_2O$, 0.002; $NaMoO_4 \cdot 2H_2O$, 0.008; and Na_2SeO_3, 0.002.

[b]Provided 10,000 IU vitamin A as retinyl palmitate, 4,000 IU vitamin D_3, 75 IU vitamin E as *dl*-α-tocopheryl acetate, and the following amounts (milligrams per kilogram of diet) of other vitamins: thiamine·HCl, 40; riboflavin, 30; D-calcium pantothenate, 150; niacin, 300; pyridoxine·HCl, 20; *d*-biotin, 2; folic acid, 15; vitamin B_{12}, 0.3; BHT (100%), 100; and inositol, *i*, *meso*, 500.

Materials and methods — Experimental lots of fingerling lake trout (initial mean body weight, 5.3 g) were fed two concentrations of either menadione sodium bisulfite (MSB; 49% menaquinone) or menadione dimethylpyrimidinol bisulfite (MPB; 45.5% menaquinone) in a semipurified diet for 18 wk (Table 1). A total of five diets were fed: the basal diet, and the basal diet supplemented with either 1.0 or 2.0 mg of each source of vitamin K per kilogram of diet. All diets were processed by extrusion without steam in a laboratory pellet mill. The pellets were crumbled into granules and graded through sieves into two sizes according to diameter of granule. The smaller granule (diam, 1.08–2.83 mm) was fed until the fish weighed about 15.0 g, after which the larger size (2.84–3.17 mm) was fed.

Each diet was fed to randomly assigned triplicate lots of 50 lake trout, held in 7-liter, Plexiglas® jars supplied with aerated well water (14 C) at a flow of 2 liters/min. Fish were fed at levels equivalent to 3% body wt daily (Deuel et al. 1952) for the first 6 wk. This percentage was progressively reduced to a minimum of 2.3 by the end of the study, based on total body weights obtained every 2 wk.

At the end of the study, five fish from each jar were used for determination of coagulation time of whole blood according to the procedure described by Poston (1964). The procedure entailed the insertion of a pointed nonheparin-coated capillary tube (1.0–1.25 mm OD) into the fish's heart caudally from the gill arches. After the capillary tube was filled with blood, segments of the tube were broken at 15-s intervals until a fibrous strand indicated that coagulation had occurred.

Blood samples for PCV determinations were taken in pointed, heparin-coated capillary tubes from five other fish from each jar and centrifuged at 13,000 × *g* for 5 min.

Experimental data were analyzed by analysis of variance and Duncan's multiple range test (Steel and Torrie 1960).

TABLE 2. Effect of source and concentration of dietary vitamin K on coagulation time and packed cell volume of lake trout blood. Means sharing the same letter (A, B, C) are similar ($P < 0.05$).

Treatment	Coagulation time[a] (*s*)	Packed cell vol (%)
Basal diet	100(A)	28.8 (A)
+ 1 ppm MPB[b]	75(B)	34.5 (B, C)
+ 2 ppm MPB	76(B)	31.9 (A, B)
+ 1 ppm MSB[c]	92(C)	37.1 (C)
+ 2 ppm MSB	95(C)	33.1 (B)
Pooled SE	1.52	1.02

[a]Each value is the mean of five determinations for each of three replicate lots per treatment.

[b]Trade name, Hetrazeen®; manufactured by Heterochemical Corporation, Valley Stream, New York. Reference to trade names does not imply Government endorsement of commercial products.

[c]Obtained from ICN, Nutritional Biochemical Corp., Cleveland, Ohio.

Results — Feeding supplemental MPB reduced the coagulation time significantly ($P < 0.01$), compared with feeding the basal diet alone or with supplemental MSB (Table 2). Supplementation of the basal diet with MSB also reduced coagulation time significantly ($P < 0.01$), but not as effectively as MPB. The feeding of 1 ppm of MPB or MSB was as effective as 2 ppm of each respective analogue of vitamin K in hastening blood coagulation.

Fish fed 1 ppm of MSB had the highest mean PCV value; although the value was not significantly different from that of fish fed 1 ppm MPB, it was significantly higher than the values for fish fed 2 ppm of either MSB or MPB.

Trout fed 2 ppm of MPB had an intermediate PCV which was not significantly different from the PCV's of fish fed either the basal diet or the basal diet plus 2 mg MSB/kg of diet.

Neither body weight nor efficiency of feed

TABLE 3. Effect of source and concentration of vitamin K on growth and feed conversion efficiency of lake trout. No significant ($P < 0.05$) differences were found.

Treatment[a]	Mean body wt after 18 wk[b] (g)	Feed:gain ratio
Basal diet	33.4	1.90
+ 1 ppm MPB	32.6	1.92
+ 2 ppm MPB	32.4	1.96
+ 1 ppm MSB	32.5	1.92
+ 2 ppm MSB	32.8	1.94
Pooled SE	0.64	0.02

[a]See Table 2 for description of treatments.
[b]Mean body weight at start of experiment was 5.3 g.

utilization (i.e. feed/gain) were significantly affected by the level or source of vitamin K (Table 3).

Discussion — Results of this study suggest that MPB is a more effective source of vitamin K (menaquinone) than MSB for hastening blood coagulation in fingerling lake trout. A dietary level of 1 ppm MPB, which provides menaquinone at the rate of about 0.5 mg/kg of diet, apparently is sufficient to insure normal blood coagulation and adequate PCV values. This level of menaquinone is similar to the requirement of vitamin K_1 (0.53 mg/kg of feed) for the young chicken (National Research Council 1971).

The apparent lack of effect of dietary vitamin K on growth and survival in lake trout agrees with previous results obtained with brook trout (Poston 1964).

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Assessment of Winter Planting of Hatchery-Reared Brook Trout (*Salvelinus fontinalis*) in Small Precambrian Lakes[1]

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FRASER, J. M. 1976. Assessment of winter planting of hatchery-reared brook trout (*Salvelinus fontinalis*) in small Precambrian lakes. J. Fish. Res. Board Can. 33: 1794–1797.

Distinctively marked 8-mo-old brook trout (*Salvelinus fontinalis*) were planted in autumn, 14-mo-old in winter, and 16-mo-old in spring in 10 experiments conducted on five small Ontario lakes in 1970–73. Comparative recoveries were assessed by examining the anglers' catch and by intensive sampling with gillnets 1 mo following the spring planting. Recovery of spring-planted trout (mean 39.7%) was significantly higher ($P < 0.01$) than for winter- (15.7%) and autumn-planted trout (7.7%). Although there was evidence in one lake of predation on winter-planted trout by large brook trout and splake (*S. fontinalis* × *S. namaycush*), the factors generally responsible for the large losses of winter- and fall-planted trout have not been identified.

FRASER, J. M. 1976. Assessment of winter planting of hatchery-reared brook trout (*Salvelinus fontinalis*) in small Precambrian lakes. J. Fish. Res. Board Can. 33: 1794–1797.

Au cours de 10 expériences poursuivies dans cinq petits lacs de l'Ontario en 1970–73, des ombles de fontaine (*Salvelinus fontinalis*) âgés de 8 mois et marqués de façon distinctive furent implantés en automne, des ombles de 14 mois en hiver et des ombles de 16 mois au printemps. Nous avons évalué les recaptures comparatives par examen des prises des pêcheurs à la ligne et par échantillonnage intensif aux filets maillants 1 mois après le peuplement de printemps. Les recaptures d'ombles de fontaine implantés au printemps (moyenne 39.7%) sont nettement plus élevées ($P < 0.01$) que celle d'ombles introduits en hiver (15.7%) et en automne (7.7%). Bien que dans un lac il y ait eu évidence de prédation sur des ombles implantés en hiver par les grands ombles de fontaine et truites moulac (*S. fontinalis* × *S. namaycush*), nous n'avons pu identifier les facteurs généralement responsables des pertes élevées subies par les ombles introduits en hiver et en automne.

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ANNUAL plantings of hatchery-reared brook trout (*Salvelinus fontinalis*) in Ontario lakes have been conventionally carried out in the 4–6 wk following spring breakup of ice. Spring planting has been favored because it places the fish in the lakes at the time of accelerating growth of food organisms and of heaviest angling pressure. Also, the cool air and water temperatures in the spring facilitate transportation and planting. However, the greater availability of aircraft and trucks in winter combined with the need for thinning of trout fingerlings for winter culture have led to winter planting in several areas. Winter planting entails transporting the fish to the lake in sealed plastic bags.

It has been suggested that winter planting is unproductive. Dahl (1934) noted that two winter plantings of brown trout (*Salmo trutta*) fry in a Norwegian lake failed to increase the number of a year-class, whereas similar open water plantings markedly increased the number of fish. Micklus and Johnson (1965) mentioned that an experimental winter planting of rainbow trout (*S. gairdneri*) fry resulted in complete mortality. Similar results were documented by Cordone and Nicola (1970) and Mullan and Tompkins (1959).

In general, the usefulness of planting trout in winter, particularly yearlings, has not been adequately assessed. Our study was designed to assess the effectiveness of winter planting by comparing the recoveries of winter-planted yearlings with spring-planted yearlings and with fall fingerlings planted in the same lakes.

Materials and methods — Study lakes — The lakes (Table 1), typical of hundreds routinely stocked throughout Ontario, are ice-covered from December

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TABLE 1. Characteristics of the lakes (number of determinations in parentheses) in which brook trout (*Salvelinus fontinalis*) were planted. (Total alk. = total alkalinity; TDS = total dissolved solids.)

Lake	Area (*ha*)	Depth		Secchi disc (*m*)	pH	Total alk. (*ppm*)	TDS (*ppm*)
		Max. (*m*)	Mean (*m*)				
Shallnot	9.3	7.3	3.0	2.1(5)	6.5(3)	8(4)	36(4)
Billy	93.0	8.5	4.6	4.7(3)	6.7(6)	12(3)	47(3)
Sawlog	6.3	8.5	4.3	4.3(13)	6.7(6)	9(3)	33(3)
Little Major	2.9	11.0	4.8	2.5(12)	5.9(7)	7(4)	35(4)
Oram	27.1	18.3	5.2	4.4(16)	6.8(4)	13(5)	42(5)

to April. Although depletion of dissolved oxygen occurs in the bottom waters during this period, determinations from water samples taken at the time of winter planting indicate adequate oxygen for trout in four of the lakes (>5 ppm) and a marginal concentration (3 ppm) in Shallnot Lake.

The fish community in four study lakes consists of four–five cyprinid species and brook trout from earlier plantings. Billy Lake supports, in addition, brown bullheads (*Ictalurus nebulosus*) and planted F_1 splake (*Salvelinus namaycush* × *S. fontinalis*) and rainbow trout (*Salmo gairdneri*). All lakes except Shallnot are fished by anglers.

Plantings — The brook trout were reared at the Pembroke Trout Rearing Station from eyed eggs produced by domestic stock at the Hills Lake Hatchery. Prior to stocking the fish were finclipped, counted into lots, and held under observation for 1–6 days. Samples of fish were dipnetted from rearing troughs, and fork lengths (Table 2) were measured to the nearest 2.5 mm.

Eight-month-old trout averaging 9.3–11.3 cm long were planted in September; 14-mo-old trout (13.7–16.7 cm) in March and 16-mo-old trout (15.7–17.8 cm) in May (Table 2). In the spring and fall, trout were transported by truck and released at a single location on each lakeshore. In winter, trout were placed in plastic bags (60 × 90 cm) and transported either by aircraft or truck and snowmobile. Each bag contained 4.5-kg trout and 13.6-kg water and was inflated with oxygen before being sealed. Transportation time between the hatchery and the lake varied from 1 to 2.5 h.

Equal numbers of yearling trout were planted in winter and spring except in the winter of 1973 when extra fish were inadvertently planted in Little Major and Sawlog lakes (Table 2). The much smaller trout of the autumn plantings were planted in greater numbers.

Recovery of plantings — Brook trout were recovered by angling and gillnetting. Anglers were interviewed and their catches examined for finclipped trout twice daily throughout the angling season (May–September).

Intensive gillnetting with panels of 25-, 38-, and 51-mm mesh monofilament nets (stretched measure) followed 1 mo after the spring plantings. Each panel was 15.2 m long by 1.8 m deep. Later in the summer standard gangs (38, 51, 64, and 76 mm) of monofilament gillnet were fished. Gillnetting provided over 50% of the trout sample from four study lakes and 100% of the sample from Shallnot Lake (Table 3). Trout caught in the gillnets were measured, weighed, and examined for finclips.

Results — In all experiments, spring-planted trout were recovered in greater numbers than trout planted 2 mo earlier through the ice (Table 2). Differences in recovery between spring-planted and winter-planted trout were analysed by the *t*-test and the resulting value of 5.81 (9 df) indicated highly significant differences in recovery.

Difference in recovery varied from lake to lake and from year to year in certain lakes (Table 2). The return of the 1970 spring planting in Billy Lake, for example, was over 4 times the return of the winter plantings. In 1971 the difference was even greater — 13 spring-planted were recovered for each winter-planted trout. The single experiments in Oram and Shallnot lakes resulted in ratios of 3:1 and 10:1, respectively, in favor of spring-planted fish. The mean recovery ratio in both Sawlog and Little Major lakes was two spring-planted to one winter-planted trout.

The recoveries of the autumn-planted trout were also low in comparison to recoveries of spring yearlings (Table 2). However, in four of eight comparisons autumn-planted fish were caught at slightly higher rates than the winter-planted trout (Sawlog 1973; Little Major 1973; Shallnot 1970; Oram 1972). Two years of plantings in Billy Lake resulted in poor recoveries (2.3–5.6%) of autumn and winter-planted fish. Only in Sawlog Lake did the recovery of winter plantings significantly ($P < 0.001$) exceed that of the autum plantings. Chi-square of pooled data on Sawlog Lake for 1971 and 1972 was 30.20 (1 df). Recoveries of the 1971 and 1972 winter plantings in Little Major Lake were also high, but no autumn plantings had been made for comparison.

TABLE 2. Comparative recoveries by gillnetting and angling of brook trout planted in autumn, winter, and spring in five Ontario lakes.

	Billy		Sawlog			Little Major			Shallnot	Oram
	1970	1971	1971	1972	1973	1971	1972	1973	1970	1972
					Spring (year n)					
No. planted	2000	2000	500	500	500	500	500	500	500	1000
$\bar{x}$ length (*cm*)	16.8	15.7	15.7	17.8	16.8	15.7	17.8	16.8	16.8	17.8
No. recovered (*yr n*)	342	771	192	224	206	209	300	218	64	258
No. recovered (*yr n+1*)	86	69	12	1	5	46	21	36	5	0
No. recovered (total)	428	840	204	225	211	255	321	254	69	258
% recovered	21.4	42.0	40.8	45.0	42.2	51.0	64.2	50.8	13.8	25.8
$\bar{x}$ length (*cm*) — yr n[a]	20.1	19.2	17.7	19.3	17.9	17.2	18.3	17.3	25.5	20.1
% increase in length	20	22	13	8	7	10	3	3	52	13
					Winter (year n)					
No. planted	2000	2000	500	500	1000	500	500	850	500	1000
$\bar{x}$ length (*cm*)	15.2	13.7	13.7	16.7	15.0	13.7	16.7	15.0	15.2	16.7
No. recovered (*yr n*)	100	49	103	141	98	173	100	42	7	87
No. recovered (*yr n+1*)	11	13	6	16	0	54	25	1	0	0
No. recovered (total)	111	62	109	157	98	227	125	43	7	87
% recovered	5.6	3.1	21.8	31.4	9.8[b]	45.4	25.0	5.1	1.4	8.7
$\bar{x}$ length (*cm*) — yr n	18.7	18.7	17.4	19.3	17.0	16.8	17.8	16.5	23.7	20.0
% increase in length	23	36	27	16	13	23	7	10	56	20
					Autumn (year n-1)					
No. planted	2000	3000	1600	1600	1600			500	300	1000
$\bar{x}$ recovered (*cm*)	11.3	9.3	9.3	9.5	10.3			10.3	11.3	9.5
No. recovered (*yr n*)	78	65	199	150	169			31	6	92
No. recovered (*yr n+1*)	8	3	9	15	9			17	4	0
No. recovered (total)	86	68	208	165	178			48	10	92
% recovered	2.9	2.3	13.0	10.3	11.1			9.6	3.3	9.2
$\bar{x}$ length (*cm*) — yr n	20.1	21.8	18.6	17.3	16.5			16.4	25.5	20.7
% increase in length	78	134	100	82	60			59	126	118

[a]Fish caught in June gillnetting (except Shallnot, Aug. 10, 1970). Mean lengths based on samples ranging from 17–519 fish.

[b]Predatory trout added — see text.

TABLE 3. Fishing pressure exerted on experimental plantings in years noted.

Lake	Year	Gillnetting[a] (*m/ha*)	Angling (*h/ha*)	% of sample gillnetted
Little Major	1971	231	155	33
	1972	52	177	35
	1973	189	78	80
Sawlog	1971	34	96	48
	1972	22	73	27
	1973	87	93	58
Shallnot	1970	131	—	100
Oram	1972	133	18	74
Billy	1970	16	35	66
	1971	21	26	86

[a]Gillnet set overnight.

While trout from all plantings grew after being planted, the survivors of the fall fingerling plants were exceptional and when captured the following June were as large as the winter and spring-planted trout (Table 2). Mean increases in length (Shallnot Lake excepted) were 11, 19, and 91%, respectively, for spring-, winter-, and fall-planted trout.

Discussion — Results of our tests clearly indicate poorer survival of brook trout planted through the ice compared to the survival of trout planted 2 mo later in open water in the same lakes. Since the winter-planted fish were slightly smaller (Table 2) and were removed from the hatchery environment 2 mo earlier than those planted in the spring, a slightly lower recovery might be expected. However, in compensation, the winter-planted fish had the benefit of a 2-mo adjustment period in the lake free from attack by fish-eating birds such as the common loon (*Gavia immer*) and American merganser (*Mergus merganser*).

Factors limiting the survival of the winter plantings are not manifest, but in Billy Lake there is evidence of predation on planted trout by large F_1 splake and brook trout — survivors of earlier plantings. Four of 25 F_1 splake examined in the 1970 Billy Lake creel census prior to spring planting contained planted brook trout, 15.0–17.3 cm long. The piscivorous F_1 splake ranged from 38.5 to 44.7 cm long and weighed approximately 800–1100 g. To further investigate, gillnets were set in the vicinity of the planting hole in Billy Lake at the time of winter planting in 1971 and caught 35 rainbow trout, 12 brook trout, and 2 F_1 splake. One splake (39.6 cm) had eaten two recently planted brook trout. An 18-cm planted brook trout was found in the stomach of a 39.0-cm brook trout. None of the rainbow trout (11 exceeded 38 cm long) contained planted trout.

Since splake were not planted in the four smaller lakes and few planted brook trout survived more than 1 yr, predation by larger trout in these lakes was probably minimal. An exception was the experimental transplanting of 25 large, wild brook trout, averaging 42.3 cm long to Sawlog Lake in October, 1972. The 1973 winter planting of yearlings that cohabited the lake with these large trout was apparently drastically reduced since only 9.8% were later recovered. In contrast, the recoveries of the 1971 and 1972 Sawlog Lake winter plantings, which had few predatory fish to contend with, were 21.8 and 31.4%, respectively.

Although autumn-planted fingerlings were only one-third the size (weight) of the winter-planted yearlings and were removed from the protection of the hatchery 5 mo earlier, their recovery (mean 7.7%) was not significantly different from that of the winter-planted trout (mean 10.8%) in the eight comparisons.

The results of our experiments clearly indicate that planting yearling brook trout through the ice of small Precambrian lakes yields relatively poor returns. The same fish, held 2 mo longer in the hatchery and planted in open water, will be recovered in significantly greater numbers. Plantings of smaller, less expensive fingerlings in the autumn is also an alternative worthy of consideration.

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Identification of Four Northern Blennioid Fish Larvae in the Canadian Atlantic Ocean (Stichaeidae, Lumpenidae)

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FABER, D. J. 1976. Identification of four northern blennioid fish larvae in the Canadian Atlantic Ocean (Stichaeidae, Lumpenidae) J. Fish. Res. Board Can. 33: 1798–1802.

Four similar northern blennioid fish larvae from the Gulf of St. Lawrence can be identified on the basis of morphological features. The two larvae of the family Stichaeidae, *Ulvaria subbifurcata* and *Stichaeus punctatus*, can be distinguished from the two larvae of the family Lumpenidae, *Leptoclinus maculatus* and *Lumpenus lampretaeformis*, by total myomere counts, the position of intestinal myomeres, presence or absence of head melanophores, and presence or absence of internal melanophores along the abdominal part of the notochord. The identification of individual species is based mainly on myomere counts and ventromedial melanophore counts.

FABER, D. F. 1976. Identification of four northern blennioid fish larvae in the Canadian Atlantic Ocean (Stichaeidae, Lumpenidae). J. Fish. Res. Board Can. 33: 1798–1802.

Certains caractères morphologiques permettent d'identifier quatre larves semblables de blennioides septentrionaux du golfe Saint-Laurent. Les deux larves de la famille Stichaeidae, *Ulvaria subbifurcata* et *Stichaeus punctatus*, peuvent être séparées des deux larves de la famille Lumpenidae, *Leptoclinus maculatus* et *Lumpenus lampretaeformis*, par le nombre de myomères totaux, la position des myomères intestinaux, la présence ou l'absence de mélanophores sur la tête et la présence ou l'absence de mélanophores internes le long de la partie abdominale de la notocorde. L'identification d'espèces individuelles est fondée surtout sur le nombre de myomères et sur le nombre de mélanophores ventro-médiaux.

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NORTHERN blennioid fish are small benthic or benthopelagic forms not often caught in nets. Although a number of illustrations of larvae belonging to members of this group have been published in the past, their exact identification in some instances have been subject to question. Numerous specimens of blennioid larvae taken with tow nets in the Gulf of St. Lawrence (Kohler et al. 1974a, b, 1975) during April, May, and June have provided an opportunity to examine and identify several species. The identity of the larval specimens taken by tow nets has been determined by carefully comparing morphological and meristic characteristics of juvenile fishes which were taken at the same time. Although the larvae of all the blennioid species recorded in the Gulf of St. Lawrence have not been collected in sufficient numbers for documentation, this note can clarify some past uncertainties in the literature.

Makushok (1958) subdivided the pricklebacks, family Stichaeidae, into eight subfamilies, but subsequently he (in Hureau and Monod 1973) restricted the Stichaeidae to the Stichaeinae and the Chirolophinae and elevated the Lumpeninae to family status, i.e. Lumpenidae, presumably including the remainder of the subfamilies. Previously, Andriyashev (1954) also considered these species within two families, Stichaeidae and Lumpenidae. Information is provided here to allow identification of two similar-looking larvae in the family Stichaeidae, namely the radiated shanny, *Ulvaria subbifurcata* (Storer), and the Arctic shanny, *Stichaeus punctatus* (Fabricius), and two similar-looking larvae in the family Lumpenidae, namely the snakeblenny, *Lumpenus lampretaeformis* (Walbaum), and the daubed shanny, *Leptoclinus maculatus* (Fries). Detailed studies are presently underway with the larvae of these four species to further illustrate their specific differences of morphology, meristics, and pigmentation.

The larvae of these four species possess the same general distinguishing features: a tubular intestine ending immediately anterior to the middle of the body, absence of a gasbladder, caudal fin development showing a dorsal bending of the notochord, wide-based pectoral fins inserted just below the middle of the body, and pigmentation dominated by stellate melanophores lying along the intestine and a row of ventromedial

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isomeric melanophores extending from the anus to the caudal fin. The numbers of these ventromedial melanophores correspond closely to the numbers of postanal myomeres and developing finrays in the anal fin.

The two larvae of the family Stichaeidae can be distinguished from the two larvae of the family Lumpenidae by total myomere counts, position of intestinal myomeres, presence or absence of head melanophores, and presence or absence of internal melanophores along the abdominal part of the notochord. Lumpenid larvae have total myomere counts more than 55, whereas stichaeid larvae have less than 55; stichaeid larvae possess two rows of melanophores dorsal to the intestine whereas lumpenid larvae possess rows of melanophores lateral to the intestine; stichaeid larvae possess head melanophores during most of their development while lumpenid larvae lack them; and stichaeid larvae possess a row of internal melanophores along the notochord whereas lumpenid larvae lack them. Separation of these fish into two families at this time is justifiable on the basis of larval characteristics. However, as with other complex groups of fish (for example, Cottidae), morphological characteristics of families will become less distinct as the larval developments of additional species are described.

Larvae of family Stichaeidae — Species within the family Stichaeidae that have been recorded from the Gulf of St. Lawrence as adults include: *U. subbifurcata*, *S. punctatus*, and *Eumesogrammus praecisus* (Krøyer) (Leim and Scott 1966). A European stichaeid, Atlantic warbonnet (Yarrell's blenny), *Chirolophis ascanii* (Walbaum), (Ehrenbaum 1905; Rass et al. 1949) and a Pacific Ocean stichaeid, the black prickleback, *Xiphister atropurpureus* (Kittlitz) (Wourms and Evans 1974) have developmental morphologies similar to the stichaeid larvae in the Gulf of St. Lawrence. The illustration in Dannevig (1919, plate II, fig. 8) which is labeled *Chirolophis*? can be assigned to *S. punctatus*. Dannevig stated that the number of vertebrae (myomeres?) totalled 55 (13 plus 42). On the other hand, the figure that Dannevig (plate II, fig. 9) identified as *S. punctatus* is an illustration of a lumpenid larva, probably *L. maculatus*. Dunbar (1947, fig. 5) illustrated a similar lumpenid larva, which he also identified as *S. punctatus*. Backus (1957) questioned the identification of both illustrations and stated that the larvae and juveniles of *S. punctatus* that he collected in Labrador "in no way resemble Dunbar's figure of a specimen 22 mm long or Dannevig's figure of a specimen 30 mm long." Both illustrations closely resemble the characteristics of specimens of *L. maculatus* collected in the Gulf of St. Lawrence. Thus, only the illustration in Dannevig (1919), labeled *Chirolophis*, is a stage in the development of *S. punctatus*. Illustrations of the larvae of *U. subbifurcata* are shown in Colton and Marak (1969) but are mistakenly identified as the snakeblenny, *Lumpenus lampretaeformis*.

The larvae and juveniles obtained from tow-net collections from the Gulf of St. Lawrence were identified as either *S. punctatus* or *U. subbifurcata*. No larvae or juveniles of *E. praecisus* were ever recognized. Larvae of both *S. punctatus* and *U. subbifurcata* possess the same general distinguishing features; at shorter lengths both species possess the internal dorsomedial line of melanophores along the notochord shown on the 7.2-mm larvae of *U. subbifurcata* and at longer lengths develop the double line of dorsal melanophores shown on the 13.5-mm larva of *S. punctatus* (Fig. 1). The larvae of *U. subbifurcata* can be distinguished from the larvae of *S. punctatus* by morphological characteristics. *U. subbifurcata* larvae have myomere counts that are less than 50 (usually 45–49), while *S. punctatus* larvae have myomere counts that are more than 50 (51–55). Postanal myomeres, as well as ventromedial melanophores, of *U. subbifurcata* number less (28–33) than those on *S. punctatus* (33–37). In addition, *U. subbifurcata* larvae lack the lateral oblique pigment lines that are obvious on *S. punctatus* larvae.

Larvae of family Lumpenidae — Species within the family Lumpenidae that have been recorded from the Gulf of St. Lawrence as adults include: *L. lampretaeformis*, *L. fabricii* (Valenciennes), *Leptoclinus maculatus*, and *Anisarchus medius* (Reinhardt) (Leim and Scott 1966). The American Fisheries Society (1970) Special Publication No. 6 uses *Lumpenus* for the genera that Makushok (1958), Hureau and Monod (1973), Legendre et al. (1975), and I refer to as *Leptoclinus* and *Anisarchus*. Also, Makushok (1958) uses the family Lumpenidae, whereas the American Fisheries Society includes these species within the family Stichaeidae. In the AFS Special Publication No. 6 *Lumpenus lampretaeformis* (Walbaum) is spelled *lumpretaeformis* rather than *lampretaeformis*. Andriyashev (1954, p. 264, English translation) explains that a misprint of the species name occurred in the original description by Walbaum and I am accepting Andriyashev's view (and Hureau and Monod 1970) that *lampretaeformis* is the correct spelling. The illustrations of *L. lampretaeformis* in Dunbar (1947, fig. 4) from Labrador and in Ehrenbaum (1905, fig. 33) from the Baltic Sea agree with the morphological characteristics of our specimens

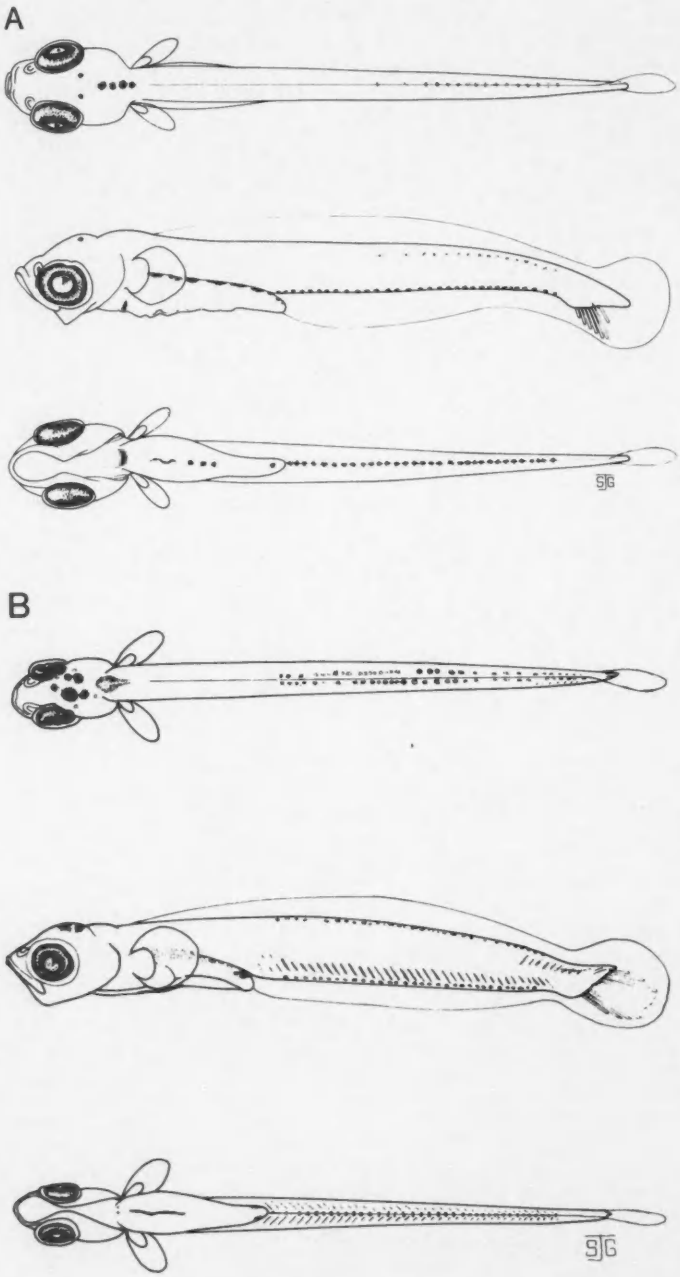

FIG. 1. Dorsal, lateral, and ventral views of larvae of A, *Ulvaria subbifurcata* (7.2-mm total length) and B, *Stichaeus punctatus* (13.5 mm total length) from the Gulf of St. Lawrence.

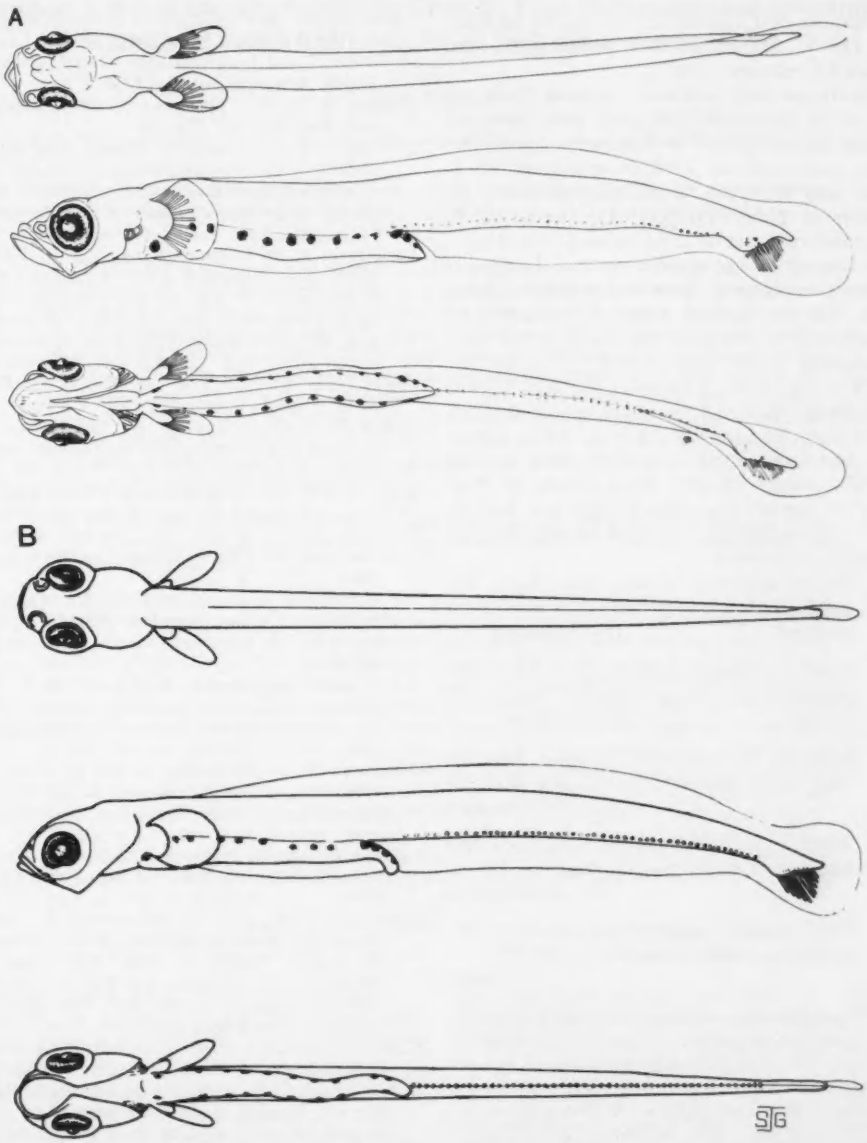

FIG. 2. Dorsal, lateral, and ventral views of larvae of A, *Leptoclinus maculatus* (13.5-mm total length) and B, *Lumpenus lampretaeformis* (16-mm total length) from the Gulf of St. Lawrence.

of *L. lampretaeformis* from the Gulf of St. Lawrence. However, the illustration in Dannevig (1919, plate II, fig. 9) identified as *S. punctatus* and Dunbar's (1947, fig. 5) illustration of *S. punctatus* are similar to specimens of *Leptoclinus maculatus*, as mentioned previously. The illustration by Rass et al. (1949, fig. 14c) of *L. maculatus* is similar to larvae collected in the Gulf of St. Lawrence. The illustration of *Lumpenus* sp. (?*medius* Rhdt) in Ehrenbaum (1905, fig. 34) is also quite similar to our specimens of *Leptoclinus maculatus*. Thus, illustrations of larvae in the

development of *L. maculatus* are shown in Dannevig (1919), Dunbar (1947), Rass (1949), and possibly Ehrenbaum (1905).

Most larvae and juveniles obtained from the Gulf of St. Lawrence collection were identified as either *L. maculatus* or *Lumpenus lampretaeformis*. Less than six juvenile specimens of *L. fabricii* and *A. medius* were identiefid solely on the basis of finray numbers. The larvae of *L. lampretaeformis* can be differentiated from *Leptoclinus maculatus* by meristic counts. *Lumpenus lampretaeformis* larvae have ventromedial melanophores that are greater than 45 (usually 46–60), whereas *Leptoclinus maculatus* larvae have melanophore counts less than 45 (usually 30–40) (Fig. 2). Also, *Lumpenus lampretaeformis* larvae possess postanal myomere counts that are greater than 50 (usually 58–63), while *Leptoclinus maculatus* larvae have counts that are less than 50 (usually 38–44). Total counts of myomeres, of course, also separate the two species.

Key to four pelagic blennioid larvae from the Gulf of St. Lawrence:

1a Total myomere counts less than 60; melanophores along intestine dorsal to intestine ..... (Stichaeidae) 2

1b Total myomere counts more than 60; melanophores along intestine lateral to intestine .... (Lumpenidae) 3

2a Presence of numerous oblique pigment lines; total myomere counts less than 50 ..... *S. punctatus*

2b Absence of lateral oblique pigment lines; total myomere counts less than 50 ..... *U. subbifurcata*

3a Ventromedial melanophores less than 45; postanal myomere counts less than 50 .... *L. maculatus*

3b Ventromedial melanophores more than 45; postanal myomere counts more than 50 ..... *Lumpenus lampretaeformis*

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Optimum Level of Dietary Biotin for Growth, Feed Utilization, and Swimming Stamina of Fingerling Lake Trout (*Salvelinus namaycush*)[1]

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POSTON, H. A. 1976. Optimum level of dietary biotin for growth, feed utilization, and swimming stamina of fingerling lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33: 1803–1806.

Triplicate lots of fingerling lake trout (*Salvelinus namaycush*) held at 9 C for 20 wk were fed a semipurified basal diet supplemented with 1% spray-dried egg white or d-biotin at concentrations of 0.1, 0.5, 1.0, or 5.0 ppm. Trout fed the basal diet, either alone or with egg white, grew more slowly and converted feed less efficiently ($P < 0.05$) than those fed supplemental biotin. Neither the growth rate nor feed conversion differed significantly among the four groups fed supplemental biotin. However, when forced to swim to exhaustion against controlled water currents, trout fed either basal diet, with or without egg white, or 0.1 ppm supplemental biotin, swam a shorter distance ($P < 0.05$) than those fed more biotin. Fish fed 0.5 ppm biotin swam as far as those fed 1.0 ppm, but not as far as those fed 5.0 ppm. These results indicate that young lake trout probably need no more than 0.1 ppm biotin for optimum growth and feed conversion, but require from 0.5 to 1.0 ppm for optimum swimming stamina.

POSTON, H. A. 1976. Optimum level of dietary biotin for growth, feed utilization, and swimming stamina of fingerling lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 33: 1803–1806.

Nous avons donné à des groupes en triplicata de fingerlings de touladi (*Salvelinus namaycush*) maintenus à 9 C pendant 20 semaines un régime alimentaire basal semi-purifié auquel on a ajouté 1% de blanc d'œuf séché par pulvérisation ou de la d-biotine à des concentrations de 0.1, 0.5, 1.0 ou 5.0 ppm. Les touladis nourris au régime basal, soit seul soit avec blanc d'œuf, croissent plus lentement et convertissent les aliments moins efficacement ($P < 0.05$) que ceux qui reçoivent un supplément de biotine. Le rythme de croissance et la conversion des aliments ne diffèrent pas de façon significative parmi les quatre groupes nourris à un supplément de biotine. Cependant, lorsque soumis à une nage forcée jusqu'à épuisement contre des courants d'eau contrôlés, les touladis nourris soit au régime basal, avec ou sans blanc d'œuf, soit à 0.1 ppm de biotine supplémentaire couvrent une distance plus courte ($P < 0.05$) que les touladis qui reçoivent plus de biotine. Les poissons nourris à 0.5 ppm de biotine nagent aussi loin que ceux qui reçoivent 1.0 ppm, mais pas aussi loin que ceux auxquels on donne 5.0 ppm. Ces résultats indiquent que les jeunes touladis ont probablement besoin de plus de 0.1 ppm de biotine pour une croissance et une conversion d'ailments optimums, mais requièrent de 0.5 à 1.0 ppm pour une vigueur de nage optimum.

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IN earlier studies, based either on meat and dry meal diets, or on high-moisture (≥70%) semipurified diets, McLaren et al. (1947), Phillips et al. (1950), Halver (1957), and Ogino et al. (1970) showed biotin to be essential for normal growth, appetite, and maintenance of normal dermal and muscle tissues in fishes. In more recent work, Poston and McCartney (1974) showed that a deficiency of biotin caused a marked reduction in liver acetyl CoA carboxylase and pyruvate carboxylase, and in swimming stamina of brook trout, *Salvelinus fontinalis*.

The wide range of recommended levels of biotin to feed salmonids (Wolf 1951; Phillips et al. 1959; Kitamura et al. 1967; Phillips 1970; National Research Council 1973), carp (*Cyprinus carpio*) (Ogino et al. 1970) and catfish (Dupree 1966), the recent transition to fish feeds of higher nutrient density, and the current high cost of synthetically produced biotin all indicate a need for further evaluation of the biotin requirements of fish fed a low-moisture, semipurified diet pelleted under conditions which prevail when manufacturing practical production diets.

This study was conducted to determine the optimum level of biotin required for growth, efficiency of feed utilization, and swimming

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TABLE 1. Composition of basal diet.[a]

Ingredient	Percent
Casein, vitamin-free	40
Gelatin	10
Soy Oil	10
Sucrose	10
Dextrin	10
Cellulose	12
Minerals[b]	6.9
Vitamins[c]	0.9
L-tryptophan	0.04
DL-Methionine	0.20

[a]Microbiological assay showed that the basal diet contained 0.02 ppm biotin. Microbiological assays were conducted by Hoffman-La-Roche, Inc., Nutley, N.J. 07110, and Agway Marketing Research Laboratory, Agway Inc., Ithaca, N.Y. 14850.

[b]Provided the following in grams per kilogram of diet: $CaHPO_4 \cdot 2H_2O$, 18.04; $CaCO_3$, 19.04; KH_2PO_4, 14.03; $NaHCO_3$, 8.82; NaCl, 5.0; $MnSO_4 \cdot H_2O$, 0.35; $FeSO_4 \cdot 7H_2O$, 0.50; $MgSO_4$, 3.02; KIO_3, 0.01; $CuSO_4 \cdot 5H_2O$, 0.03; $ZnCO_3$, 0.15; $CoCl_2 \cdot 6H_2O$, 0.002; $NaMoO_4 \cdot 2H_2O$, 0.008; Na_2SeO_3, 0.002.

[c]Provided 10,000 IU vitamin A as retinl palmitate, 4,000 IU vitamin D_3, 75 IU vitamin E as *dl*-α-tocopheryl acetate, and the following amounts (milligrams) of other vitamins per kilogram of diet: thiamine·HCl, 40; riboflavin, 30; D-calcium pantothenate, 150; niacin, 300; pyridoxine·HCl, 20; folic acid, 15; vitamin B_{12}, 0.3; butylated hydroxytoluene (100%), 100; inositol, *i, meso*, 500; vitamin K as menadione dimethylpyrimidinol bisulfite, 22.

stamina in fingerling lake trout (*Salvelinus namaycush*) fed a pelleted, low-moisture (<10%) diet.

Materials and methods — A 20-wk study was conducted with 2-mo-old lake trout, hatched and reared at the Tunison Laboratory of Fish Nutrition, from eggs taken from brood stock originating from Lake Michigan and maintained at the Marquette (Michigan) State Hatchery. The experimental trout, which had a mean weight of 2.2 g at the start of the study, were fed graded levels of crystalline d-biotin in a semipurified diet (Table 1) containing 4.7 ± 0.6% moisture on an air-dry basis. The basal diet was supplemented with either raw, spray-dried egg white at 1% of the diet, or d-biotin at 0.1, 0.5, 1.0, or 5.0 mg/kg of diet. All diets were processed by extrusion, without steam, in a laboratory pellet mill, crumbled into granules, and graded through sieves into two sizes. The smaller granules (diam, 1.2–2.0 mm) were fed until the fish weighed about 4.5 g; thereafter, the larger-size granules (2.1–3.4 mm) were fed.

Each diet was fed to randomly assigned triplicate lots of 50 lake trout each, held in 7-liter plexiglass jars supplied with aerated well water (9 C) at a flow of 2 liters/min. Fish were fed at levels equivalent to 3% body wt daily, as determined by the method of Deuel et al. (1952), for the first 6 wk; the amount fed was then gradually reduced to a minimum of 2.2% body wt by the last 2 wk of study, based on total body weights obtained at 2-wk intervals.

At the end of the study, 30 fish from each jar were tested for swimming endurance by being forced to swim to exhaustion against controlled water currents in a stamina-testing apparatus (Poston and McCartney 1974). A pooled sample of 10 fish per jar was analyzed for dry matter, ash, fat, and protein. Five fish from each jar were examined histologically by R. L. Herman (Eastern Fish Disease Laboratory, Leetown [Kearneysville], W. Va.) for determination of the possible effect of the level of biotin in fish tissues.

Experimental data were subjected to analysis of variance and Duncan's multiple range test (Steel and Torrie 1960).

Influence of diet on growth, feed conversion, stamina, and survival of lake trout — Trout fed the basal diet, either alone or with egg white, grew more slowly than those fed 0.1 or 0.5 ppm supplemental biotin. Fish fed the higher biotin levels (1.0 or 5.0 ppm) gained at rates between those fed the basal diet and those fed the two lower biotin levels. The two intermediate rates of gain, however, were not different ($P < 0.05$) from either the high or low values. Feeding supplemental biotin increased the food conversion efficiency also. There was a trend for the fish to convert feed to flesh less efficiently as the level of supplemental biotin progressed from 0.1 to 5.0 ppm (Table 2).

When forced to swim to exhaustion, however, those fed either the basal diet (with or without egg white) or 0.1 ppm of supplemental biotin swam a significantly shorter distance (i.e., mean time spent in stamina apparatus × mean velocity of water current) than did those fed more biotin. The distance swum by fish fed 0.5 ppm biotin was not significantly different from that swum by those fed 1.0 ppm biotin, but was significantly ($P < 0.05$) less than for those fed 5.0 ppm biotin.

Mortality was low in all experimental lots of fish. A total of only 11 fish died during the entire study.

Influence of diet on body composition — Results from proximate analyses showed a trend for trout fed the basal diet, with or without egg white,

TABLE 2. Growth, feed utilization, and swimming endurance of lake trout (*Salvelinus namaycush*) fed graded levels of biotin. Means sharing the same letter are not significantly different from each other ($P < 0.05$). Initial mean weight was 2.2 g.

Biotin Added (mg/kg of diet)	Body wt gain (%)	20-wk feed/gain	Distance swum (*m*)
None	582a	1.94a	270a
None + 1% egg white	573a	1.89a, b	252a
0.1	690b	1.71c	256a
0.5	667b	1.72c	296b
1.0	650a, b	1.73c	315b, c
5.0	645a, b	1.78b, c	323c
Pooled SE	21.5	0.03	6.5

TABLE 3. Composition of lake trout fed graded levels of biotin. Means sharing the same letter are not significantly different from each other ($P < 0.05$).

Biotin added (mg/kg of diet)	Carcass dry matter (%)	Carcass fat (% of dry matter)
None	25.6a	6.2a
None + 1% egg white	25.7a	6.1a
0.1	26.6a	7.4b
0.5	26.6a	7.2a, b
1.0	26.2a	6.6a
5.0	26.1a	6.7a
Pooled SE	0.33	0.28

to contain less dry matter than those fed other diets (Table 3). These differences, however, were not significant. Fish fed either 0.1 or 0.5 ppm biotin had significantly more body fat than did fish fed the other diets.

Histological examination of the livers from trout fed no supplemental biotin showed extensive glycogen-type vacuoles which obscured much of the cellular cytoplasm. Liver vacuolation diminished as the quantity of supplementary dietary biotin increased. There was no histological evidence of fat infiltration of livers or of the abnormal skin disorder, "blue slime" disease, reported earlier in biotin-deficient brown trout (*Salmo trutta*) and brook trout (Phillips et al. 1951, 1953).

Discussion — Results of this study confirm the findings of Phillips et al. (1957) that lake trout require dietary biotin for normal growth and food conversion. However, the data suggest that the optimal level of biotin required by young lake trout varies according to the function or performance measured.

The level of biotin required for normal growth and feed conversion in this study is within the range (0.05–0.25 ppm) reported by McLaren et al. (1947) for rainbow trout (*Salmo gairdneri*). However, it is substantially lower than the levels previously suggested for salmonids (Halver 1972; National Research Council 1973) and carp (Ogino et al. 1970). Reduced growth and altered body composition of trout fed the higher levels of biotin in this study resemble results obtained by McLaren et al. (1947) with rainbow trout.

Although no previously reported quantitative biotin requirement for normal swimming stamina exists, results of this study support earlier findings (Poston and McCartney 1974) that diminished swimming stamina is a sign of biotin deficiency in trout.

Increased number of glycogen-type vacuoles in the liver of biotin-deficient trout resembles the abnormal deposition of glycogen-like granules in the kidney tubules and muscular bundles of biotin-deficient carp described by Ogino et al. (1970). Increased levels of tissue glycogen possibly resulted from a low activity of biotin-containing lipogenic and gluconeogenic enzymes, or both, in biotin-deprived trout (Poston and McCartney 1974).

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Increased Invertebrate Drift in an Experimental Stream Caused by Electrofishing

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Bisson, P. A. 1976. Increased invertebrate drift in an experimental stream caused by electrofishing. J. Fish. Res. Board Can. 33: 1806–1808.

Electrofishing stimulated a tenfold increase in total macroinvertebrate drift in an experimental stream channel. While nearly all aquatic taxa exhibited elevated drift rates during shocking, turbellarians and chironomids showed the greatest total increases. A few taxa were relatively unaffected. Except for the Chironomidae, benthic invertebrate biomasses were not significantly depressed immediately following electrofishing.

Bisson, P. A. 1976. Increased invertebrate drift in an experimental stream caused by electrofishing. J. Fish. Res. Board Can. 33: 1806–1808.

La pêche à l'électricité augmente de 10 fois la dérive totale des macro-invertébrés dans le chenal d'un cours d'eau expérimental. Alors que presque tous les taxons aquatiques manifestent des taux de dérive plus élevés au moment du choc, les turbellariés et les chironomides sont les groupes chez lesquels les augmentations totales sont les plus fortes. Quelques taxons sont relativement inaffectés. A l'exception des Chironomidae, la biomasse des invertébrés benthiques ne diminue pas de façon significative immédiatement après la pêche à l'électricité.

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Electrofishing is usually the method of choice when collecting live fish in woodland streams possessing considerable cover. But despite its widespread use, relatively little is known of the effect of electrofishing on benthic macroinvertebrate populations. This paper describes the results of a brief experiment designed to detect immediate changes in the drift of stream invertebrates in response to rather intense shocking.

Electrical stimuli have been used by some workers for collecting and sorting purposes (Bay-

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TABLE 1. Invertebrate drift (micrograms per meter^3) in the shocked and unshocked riffles. Pretreatment values are means of hourly samples taken from 0800 to 1100. Posttreatment values are means of samples taken from 1300 to 1500. Treatment values refer to the 1200 sample.

Taxon	Pretreatment		Treatment		Posttreatment	
	Shocked	Unshocked	Shocked	Unshocked	Shocked	Unshocked
Turbellaria	196	12	51120	67	646	10
Oligochaeta	278	99	1829	159	124	177
Planorbidae	244	47	1238	75	97	250
Hydracarina	55	20	32	28	22	40
Ostracoda	1194	247	1723	159	475	242
Copepoda	19	13	596	10	12	8
Collembola	3634	1049	2961	1675	3620	696
Ephemeroptera	1	4	2170	4	82	17
Plecoptera	115	70	3160	36	248	87
Trichoptera	12	6	1268	2	121	9
Chironomidae	3544	1702	19654	2016	1747	1419
Other Diptera	128	80	133	44	30	12
Misc. Aquatic	110	83	60	32	29	52
Terrestrial	28	19	79	74	20	16
Totals	9558	3451	86023	4381	7273	3035

less 1961; Ervin and Ball 1974) or for parasite control (Combs 1968), and their experiments have shown that various taxa may often react in a dissimilar manner. A corollary purpose of the study was therefore to compare the responses of different invertebrates to electrofishing and to discuss the implications of differing responses to stream sampling procedures.

Materials and methods — The experiment was carried out at the Kalama Springs Laboratory in southwestern Washington. Characteristics of the experimental stream used in the study have been described by Thut (1969). Two riffles, an upstream control and downstream treatment, were selected for comparison. The riffles were similar in size (18.6 m^2), substrate composition (mostly pebbles and cobbles), and flow (1.5 m^3/min). The only difference was that average velocity in the treatment riffle was 53 cm/s while in the control the average velocity was 43 cm/s.

Driftnets made of 210-μm mesh nylon spanned the width of the streams so that the entire flow passed through them. Nets were positioned at the upstream and downstreams ends of each of the two riffles. The upstream nets filtered out incoming drift, while the downstream nets captured only material that originated from the test riffles. Samples were taken for 15-min periods at hourly intervals commencing at 0800 and terminating at 1500 on November 5, 1975. During the 1200 sample, the treatment riffle was exposed to electrofishing for 4.5 min, or about 15 s/m^2 of riffle surface area.

A portable battery-powered pulsed DC shocker (Smith-Root Type VII electrofisher) administered 500 V shocks, each of 8 ms duration and pulsed at a frequency of 80 Hz. The low conductivity in the experimental stream (50 μmho/cm) made it necessary to use the high voltage setting to stun fish sufficiently for them to be netted. During shocking the electrodes were carefully passed over the substrate so that no mechanical disruption to invertebrates or periphyton occurred. At no time was the stream waded. Identical procedures were followed in the upstream control riffle during the 1200 sample, except that the shocker was turned off.

Drift samples were sorted under magnification and dry biomasses were determined gravimetrically. Results are expressed as micrograms of invertebrate dry weight per meter^3 of water that passed the downstream end of the riffles.

Results — The drift of nearly all groups of invertebrates increased during electrofishing (Table 1); total drift biomass in the shocked riffle was about tenfold greater than the means of pretreatment and posttreatment samples. Total biomass in the control sample at 1200 did not differ greatly from morning or afternoon averages. Even excluding the noon measurement period, the treatment riffle produced significantly more drift ($P < 0.01$, paired t-test) than the control. However, the absence of a great increase in invertebrate drift in the 1200 control sample suggests that the large numbers of invertebrates drifting in the treatment riffle at 1200 were caused by electrofishing.

Responses of various taxa to shocking differed greatly. Collembola and Hydracarina were apparently unaffected. Turbellaria showed the greatest increase, rising from 2% of the drift (by weight) before shocking to nearly 60% of the drift from the treatment riffle during shocking.

Chironomidae also exhibited especially high drift rates during shocking. A few groups (Turbellaria, Ephemeroptera, Plecoptera, Trichoptera) maintained higher drift rates throughout the 3 h following electrofishing than had been measured in morning samples. Some others showed slight declines, although similar declines were often observed in the control riffle.

Condition of the shocked invertebrates was checked visually before they were preserved. It seemed that most organisms had been stunned and carried downstream into the net before reviving; few individuals had been killed.

Four 0.017 m^2 core samples were taken from both treatment and control riffles on the day before and the day after the electrofishing experiment to determine if shocking had any short-term effect on benthic invertebrate biomasses. T-tests indicated that no significant differences in the biomasses of various taxa had occurred in the control riffle after the experiment. In the treatment riffle only Chironomidae exhibited a significant change ($P < 0.05$), decreasing from 8.0 g/m^2 before shocking to 3.9 g/m^2 after shocking. Other taxa, including Turbellaria, showed no significant declines.

Discussion — Dissimilar responses of aquatic macroinvertebrates to shocking suggest that electrical devices for attraction and sorting may be effective with some taxa and relatively ineffective with others. It is unlikely that electrofishing can be used to give quantitative estimates of total benthic biomass.

Whetner or not repeated electrofishing over the same area of a stream can significantly reduce standing stocks or alter invertebrate community structure remains to be shown. The observed decline in chironomid biomass, although statistically significant, may not have been due exclusively to the experimental treatment; even the high drift rate during shocking accounted for less than 1% of the estimated benthic biomass. Other factors requiring consideration in assessing the impact of electrofishing on invertebrate populations include knowledge of recolonization rates from upstream sources and the extent of physical disturbance to the stream substrate.

Fish collected by electrofishing are sometimes held for stomach analysis. When sampling proceeds in a downstream direction, large numbers of invertebrates dislodged by shocking drift downstream and may be consumed by fish before the fish themselves are captured. Because aquatic invertebrates are not uniformly affected by electrofishing, stomach samples taken from such fish will not represent typical food organisms. While Vincent's (1971) review of electrofishing procedures does not specify whether collecting should be done in an upstream or downstream direction, upstream collections would appear to be preferable when fish are to be retained for studies of food habits.

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Addendum — Two papers (Elliot, J. M. and T. B. Bagenal. 1972. The effects of electro-fishing on the invertebrates of a Lake District stream. Oecologia [Berlin] 9: 1–11.; Fowles, C. R. 1975. Effects of electric fishing on the invertebrate fauna of a New Zealand stream. N.Z. J. Mar. Freshwater Res. 9: 35–44.), obtained too late for inclusion, both recorded large increases in drift during electrofishing. In addition, Elliot and Bagenal (1972) noted a 30% decline in benthic invertebrate numbers after electrofishing, compared to an 8% decrease found by Fowles (1975).

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Factors Affecting Winter Respiration in Ontario Lakes

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WELCH, H. E., P. J. DILLON, AND A. SREEDHARAN. 1976. Factors affecting winter respiration in Ontario lakes. J. Fish. Res. Board Can. 33: 1809–1815.

Winter oxygen consumption was measured in 16 Ontario lakes. Whole lake respiration ranged from 0.08 to 0.39 g O_2 m^{-2} day^{-1} and was positively correlated with mean depth, phosphorus m^{-2} at spring overturn, and summer chlorophyll *a* m^{-2}. Morphological variables plus Secchi depth were explained over 80% of the variability in respiration rates.

WELCH, H. E., P. J. DILLON, AND A. SREEDHARAN. 1976. Factors affecting winter respiration in Ontario lakes. J. Fish. Res. Board Can. 33: 1809–1815.

Nous avons mesuré la consommation hivernale d'oxygène de 16 lacs de l'Ontario. La respiration des lacs entiers s'étale de 0.08 à 0.39 g $O_2 \cdot m^{-2} \cdot jour^{-1}$ et est en corrélation positive avec la profondeur moyenne, le phosphore $\cdot m^{-2}$ au moment de la circulation générale de printemps et la chlorophylle $a \cdot m^{-2}$ en été. Plus de 80% de la variabilité dans les taux de respiration s'expliquent par des variables morphologiques en plus de la profondeur du disque de Secchi.

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LIMNOLOGISTS have long been interested in the relationships between lake morphometry, nutrients, and primary and secondary production. It has been shown that lakes lying on the Canadian Precambrian Shield typically have high N:P ratios, and that phosphorus availability controls photosynthesis in those lakes up to the point where the daily carbon invasion rate becomes limiting (Schindler and Fee 1974). Further work on a group of lakes in the Haliburton area of Ontario (Fig. 1) showed that spring phosphorus concentration can be predicted from data on phosphorus loading and retention (Dillon and Rigler 1974a), and that summer chlorophyll *a* concentration can in turn be predicted from phosphorus concentration (Dillon and Rigler 1974b). In the present work we wished to explore the relationships between some of these variables and a dynamic measure of production or total energy flow.

We decided to measure the winter respiration rates of the lakes in question because of the relative ease with which such measurements can be made when compared with estimating primary production, and because we assumed that the winter respiration rate of a lake is a direct function of its total annual photosynthesis. This is shown, for example, in Char and Meretta lakes in the Canadian arctic (Kalff and Welch 1974; Welch and Kalff 1974) and implied by Hargrave's (1973) work linking primary production with benthic respiration.

Allochthonous organic input is also part of a lake's metabolic budget. The only lakes we know of where all energy sources were estimated are Marion Lake, a shallow ($\bar{z}$ = 2.4 m), small (13 ha) water body with very high flushing where autochthonous photosynthesis constitutes about 52% of the total metabolized and stored energy (Hall and Hyatt 1974), and Char Lake, where net organic import is negligible (Welch and Kalff 1974). Because most of the lakes we discuss below constitute a lake chain where organic imports are probably nearly balanced by exports and we think other sources of allochthonous material are minor, we have assumed for the purposes of this paper that net organic import is not contributing to lake respiration.

In the dark, a lake consumes oxygen in respira-

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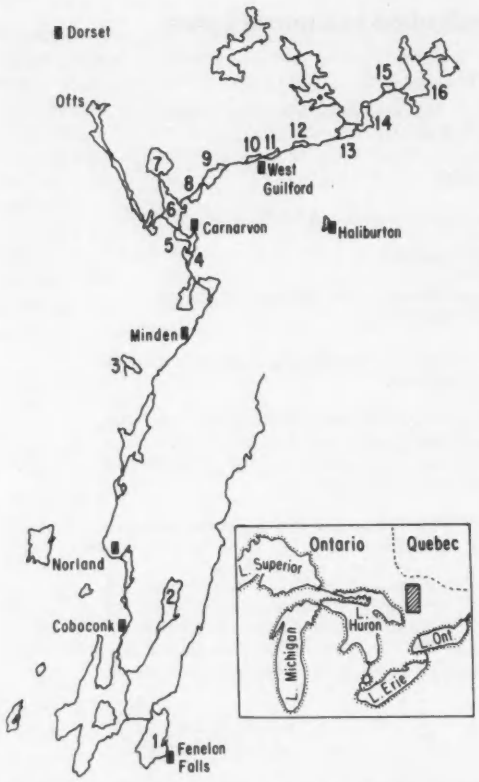

FIG. 1. Locations of the 16 lakes: 1) Cameron, 2) Four Mile, 3) Bob, 4) Twelve Mile, 5) Little Boshkung, 6) Boshkung, 7) Hall's, 8) Beech, 9) Maple, 10) Green, 11) Pine, 12) Cranberry, 13) Eagle, 14) Moose, 15) Oblong, 16) Haliburton.

tion but does not evolve oxygen by photosynthesis. If volume-based changes are sufficiently large, respiration can be measured during the dark hours of each night (Welch 1968). The dark respiration of polar lakes can also be measured because, despite the slow rate of oxygen consumption, the effective "night" may last over 6 mo (Welch 1974). The diurnal oxygen change in the average Precambrian Shield Lake is probably too slight to detect without taking a prohibitively large number of samples, but winter conditions in such lakes are somewhat like those in polar lakes, since they are ice-covered, thereby eliminating surface diffusion, and sufficiently snow-covered that photosynthesis is negligible (Schindler and Nighswander 1970). Unlike some polar lakes, in- and outflowing water can still alter the oxygen balance, although we tried to account for this potential source of error.

Materials and methods — We measured the oxygen changes in 16 Ontario lakes in the Haliburton area when they were ice-covered, January through March 1972. For oxygen, 10–20 water samples at depth intervals corresponding approximately to the depth distribution of lake volume were taken biweekly at a single station near the deepest part of each lake. Snow and ice thickness were measured at the same time. Water samples were fixed immediately and titrated 2–8 h later, essentially using the technique of Carpenter (1965). Oxygen concentrations were multiplied times lake volume for each stratum, the results summed and divided by lake area to give g O_2 m^{-2} of lake surface. Oxygen m^{-2} was regressed on time and the resultant respiration rates were compared by regression analysis with other parameters such as flushing and chlorophyll concentration. An initial analysis of the data showed that there was no detectable decrease in lake respiration rates during the winter, and that oxygen concentrations remained over 8 mg $liter^{-1}$ in most of the water mass in each lake. Welch (1974) reported constant winter respiration rates in arctic lakes down to very low oxygen levels.

Data on flushing rates, morphometry, phosphorus, and chlorophyll are from Dillon (1974) and Dillon and Rigler (1974a, b), defined as:

$$\text{flushing rate } (\rho) = \frac{\text{annual water inflow } (m^3\ yr^{-1})}{\text{lake volume } (m^3)}$$

$$\bar{z}\ \text{(mean depth)} = \frac{\text{lake volume } (m^3)}{\text{surface area } (m^2)}$$

[P] = concentration of phosphorus at the time of the spring overturn, either measured directly or predicted from the relationship $[P] = L(1 - R)/\bar{z}\ \rho$; where L = phosphorus loading, g m^{-2} yr^{-1} and R = phosphorus retention cofficient, fraction of total entering P retained by the lake

chlorophyll = average concentration of chlorophyll *a* in the epilimnion, either measured, or predicted from the relationship

$$\log_{10} [\text{chl}a] = 1.45 \log_{10} [P] - 1.14$$

where P is either measured or predicted for the 16 lakes.

Keep in mind that quantities can be transformed from area to volume-based data, or vice versa, by dividing or multiplying by the mean depth.

Results — Respiration rates per square meter (R m^{-2}) ranged from 0.08 to 0.39 g O_2 m^{-2} day^{-1} (Table 1). The SD of a single estimate of the total oxygen content of a lake varied between 2 and 11 g O_2 m^{-2} and the mean oxygen content of the lakes ranged from 65 to 321 g O_2 m^{-2}. The precision of replicate dissolved oxygen determinations on homogeneous water masses in the laboratory was always better than ±0.01 mg $liter^{-1}$, or 0.1 g m^{-2} for a lake with $\bar{z}$ = 10 m, so most of the variability for a given estimate of total oxygen was due to various sampling errors.

TABLE 1. Winter respiration rates of 16 Ontario lakes; SE in parentheses.

Lake	Winter respiration rate ($g\ O_2\ m^{-2}\ day^{-1}$)		Mean depth (m)
Beech	0.282	(0.021)	9.8
Bob	0.273	(0.021)	18.0
Boshkung	0.393	(0.023)	23.4
Cameron	0.217	(0.017)	7.1
Cranberry	0.075	(0.013)	3.5
Eagle	0.169	(0.015)	7.9
Four Mile	0.282	(0.026)	9.3
Green	0.117	(0.023)	6.1
Haliburton	0.295	(0.037)	19.6
Hall's	0.373	(0.036)	27.2
Little Boshkung	0.127	(0.041)	7.6
Maple	0.242	(0.016)	11.6
Moose	0.295	(0.066)	16.6
Oblong	0.186	(0.015)	11.2
Pine	0.097	(0.017)	7.4
Twelve Mile	0.286	(0.046)	11.5
Mean	0.232		12.4

TABLE 2. Correlation of respiration for 16 lakes with other variables.

Variable	Correlation coefficients with R m^{-2}	with R m^{-3}
Mean depth (m)	0.85	−0.47
Maximum depth	0.82	−0.47
Secchi depth	0.51	—
Flushing	−0.75	—
$\bar{z}$/area	−0.24	−0.47
N:P	0.20	—
Chlorophyll a (m^{-2})	0.71	—
Predicted from predicted phosphorus	0.74	—
Predicted from measured phosphorus	0.56	—
Phosphorus (m^{-2})		
Measured	0.79	—
Predicted	0.74	—

R m^{-2} was highly correlative with the mean and maximum depths of the lakes, whereas R m^{-3} was not (Table 2); $\bar{z}$/area, an index of "relative depth," was marginally correlated with R m^{-2} and R m^{-3} (Table 2). For these lakes, therefore, volume-based respiration was relatively constant for all lake types, with area-based respiration being a function of depth.

Area-based chlorophyll and phosphorus variables were highly correlated with R m^{-2}, except for chlorophyll estimates using measured phosphorus as a predictive variable (Table 2).

The combined effect of the various morphometric and nonmorphometric factors on R m^{-2} was tested by a regression analysis, using three approaches: a) morphometric factors only, b) nonmorphometric factors, and c) combined (Table 3). Mean depth and maximum depth

TABLE 3. Multiple regression of several variables on lake respiration, R m^{-2} (g O_2 m^{-2} day^{-1}); R = coefficient of multiple correlation; R^2 = percent variable explained.

a) Regression R m^{-2} vs. morphometric variables

Variable in regression	R^2
Mean depth (×1)	0.72 (×1)
Secchi depth (×2)	0.78 (×1 + ×2)
Flushing (×3)	0.82 (×1 + ×2 + ×3)
Maximum depth (×4)	0.83 (×1 + ×2 + ×3 + ×4)

$$R\ m^{-2} = 0.3157 + 0.0208 \times 1 - 0.0382 \times 2 - 0.0015 \times 3 - 0.0018 \times 4$$

b) Regression R m^{-2} vs. nonmorphometric variables

Variable in regression	R	R^2
Phosphorus m^{-2} (×1)	0.79	0.62 (×1)
Chlorophyll m^{-2} (×2)	0.83	0.69 (×1 + ×2)
N:P ratio (×3)	0.83	0.70 (×1 + ×2 + ×3)

c) Regression R m^{-2} vs. combination of morphometric and nonmorphometric variables

The final equation was the same as in a) above.

TABLE 4. Dissolved oxygen changes g O_2 m^{-2}.

	1700		0800		1700
Cameron Lake					
Feb. 1–2	87.01		87.36		86.99
Difference		+0.35		−0.37	
Pine Lake					
Mar. 23–24	83.29		81.31		81.78
Difference		−1.98		+0.47	
Four Mile Lake					
Jan. 21–22	111.71		111.11		111.24
Difference		−0.60		+0.13	

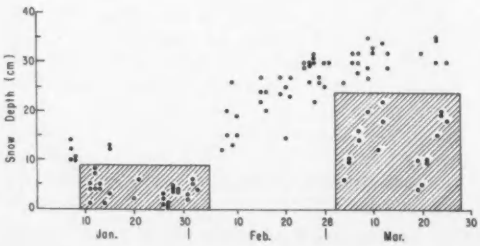

FIG. 2. Snow cover on 16 Ontario lakes, 1972. Shaded areas indicate water-soaked snow.

dominated the relationship whether they were present with other morphometric variables or in combination with morphometric and nonmorphometric factors. In the absence of lake morphometric factors, phosphorus and not chlorophyll was the dominant variable. However, when in combination with morphometric variables, including mean depth and/or maximum depth, both chlorophyll and phosphorus were of negligible value in the predictor equation.

Discussion — Reality of respiration rates — How close were these apparent respiration rates to actual winter lake respiration? Photosynthesis could have altered oxygen concentrations. Snow cover in February–March was 10–30 cm (Fig. 2), which was sufficient to reduce light transmission by 95–99% (Welch and Kalff 1974). There was no indication of lower apparent respiration during January when snow cover was light. On three occasions we also checked for diurnal differences by doing three oxygen series at 1700, 0800, and 1700. The results (Table 4) were variable. Cameron Lake increased overnight and de-

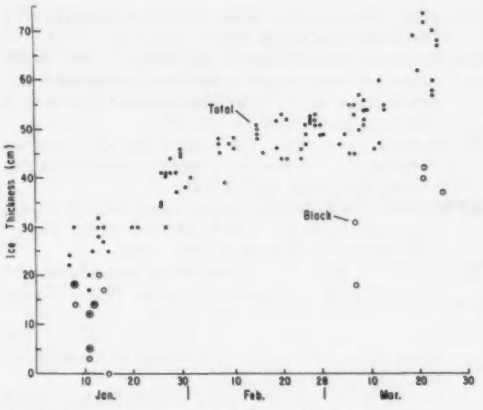

FIG. 3. Ice cover on 16 Ontario lakes, 1972. ○, "black" ice; ●, total ice including "white" ice. The ice was frequently not differeniated into the two types.

creased during the day; Pine and Four Mile showed the expected diurnal changes. The change per lake was not significant considering the error associated with these measurements (see Results section). Schindler and Nighswander (1970) stated that "winter photosynthesis was negligible under snow cover" for Clear Lake, close by the lakes discussed here. We think, therefore, that winter photosynthesis probably did not cause significant changes in apparent respiration.

Slush ice formation may also alter oxygen concentrations. When snow accumulates on lake ice to the point where the ice becomes negatively buoyant, water welling up through cracks will soak the lower snow layers, depressing the ice further until part or all of the lake surface becomes covered with a layer of slush overlaid by snow. When this layer freezes it forms slush, or "white" ice, as opposed to the clear "black" ice formed by freezing at the lower ice surface. Under normal (black) ice formation, gases are excluded from the ice with nearly 100% efficiency (Welch 1974), and the total oxygen content of the lake is not affected, whereas oxygen contained in the water incorporated in slush ice is removed from the lake.

At the beginning of the sampling program in January there was about 10 cm of slush ice present on a few lakes (Fig. 3). By late March, there was about 40 cm of black ice and 20 cm of slush ice, much of the slush ice having been formed in March as the snow cover built up. If we assume that an average of 15 cm of water was incorporated into slush ice between the first and last sampling periods, then (.15) (14 mg O_2 liter^{-1}) = about 2.1 g O_2 m^{-2} was removed in 75 days, or about .03 g O_2 m^{-2} day^{-1}, constituting 8–35% (mean = 13%) of the apparent respiration rates. There was, therefore, a small upward bias in apparent respiration rates due to slush ice formation.

Inflow–outflow of water could also have changed the oxygen concentrations as indicated by the high correlation ($r = -.76$) between flushing and oxygen consumption. Schindler (1971) reported winter respiration rates of .036–.253 g O_2 m^{-2} day^{-1} for 11 northwestern Ontario Shield lakes, all of which had flushing times in excess of 2 yr. The similarity in respiration rates for the two sets of lakes indicates that high flushing did not strongly affect the oxygen depletion rate.

The apparent respiration rates for at least the larger lakes must have been close to actual rates, (0.30 g O_2 m^{-2} day^{-1}) (365) = 110 g O_2 m^{-2} yr^{-1}, and higher summer water temperature would probably increase this to at least 150 g m^{-2} yr^{-1}, or the equivalent of 55 g C m^{-2} yr^{-1}. Schindler et al. (1973) found 83.1 and 51.0 g C m^{-2} yr^{-1} production in lakes 239 and 240 at the Experimental Lakes Area in northwestern Ontario; winter respiration rates in these two Shield lakes were 0.19 and 0.20 g O_2 m^{-2} day^{-1}. Schindler and Nighswander (1970) found a photosynthesis rate of 250 g C m^{-2} yr^{-1} in Clear Lake, on the Shield near the lakes discussed here. Both studies incorporated large filtration corrections which may not have been justified (Nalewajko and Lean 1972; McMahon 1973; Rudd and Hamilton 1973). With due allowance for increased summer metabolism, the winter respiration rates reported here are reasonable compared with production rates in other Shield lakes.

Causative factors — The overriding effect of depth could mean several things. Differential storage, with shallow lakes storing a higher proportion of their production in the sediment than do deeper lakes, would contribute toward a positive R m^{-2}:$\bar{z}$ correlation. However, storage is only a few percent of net carbon supply for Lake Ontario, 15 ha Mirror Lake in New Hampshire (Jordan and Likens 1975), and 52 ha Char Lake (DeMarch 1975), indicating that storage has a negligible effect on the correlation between lake respiration and carbon supply. Another possibility is that summer respiration is relatively more important in shallow lakes, because a shallow lake has more of its lake bottom at high summer temperatures than a deep lake with a large hypolimnion. The simplest explanation is that deep Shield lakes do in fact photosynthesize more than shallow lakes.

It is interesting that phosphorus m^{-2} and chlorophyll m^{-2} do not figure more prominently in a multiple regression of respiration on variables including depth, Secchi depth, and flushing rate (Table 4). Both phosphorus and chlorophyll concentrations exhibited a narrow range in this group of lakes, and we expect that data from a wider range of lake types would decrease the significance of depth per se and increase the significance of phosphorus or chlorophyll m^{-2}.

Predicting lake respiration — The respiration of similar lakes in Ontario can be predicted from morphometric data alone. Mean depth is the best single predictive variable but a maximum depth is nearly as good and is a datum that is easily obtained for most lakes. Using only maximum depth, g O_2 m^{-2} day^{-1} = (0.105) + (0.004) max. depth [±0.056]. For example, given a maximum depth of 25 m, R m^{-2} = (0.205) (±0.112) [95% confidence interval].

Comparison with other lakes — Brunskill and Schindler (1971), Armstrong and Schindler (1971), and Schindler (1971) gave winter oxygen depletion rates, morphometric, and chemical data for 11 Shield lakes at the Experimental Lakes Area in northwestern Ontario. Our analysis of their data indicate that oxygen depletion rates were correlated with mean depth (r = 0.47), maximum depth (r = 0.37), and summer phosphorus m^{-2} (r = 0.46), but not with chlorophyll m^{-2} (r = 0.04). These correlations will undoubtedly change as better data are published for these lakes.

Winter respiration rates for nine lakes in the high arctic (Welch 1974) showed no significant relation to maximum depth (r = 0.20), which is not unexpected considering the probable importance of other factors such as turbidity at that latitude. Phosphorus and chlorophyll data are available for two of those lakes, Char and Meretta, although the extremely seasonal nature of phosphorus addition to polluted Meretta Lake precludes further analysis. The 0.11 g O_2 m^{-2} day^{-1} respiration rate for Char Lake is low compared with the Ontario lakes' respiration: mean depth relationship (0.21 g O_2 m^{-2} day^{-1} predicted). But if 40 mg total phosphorus m^{-2} is used for Char Lake (Schindler et al. 1974), the Ontario lakes' data predict a respiration of 0.13 g O_2 m^{-2} day^{-1}, which is close to the actual rate.

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Preferred Temperature of Fish: a New Method

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MÜLLER, R., AND F. E. J. FRY. 1976. Preferred temperature of fish: a new method. J. Fish. Res. Board Can. 33: 1815–1817.

A simple apparatus for establishing a short, steep vertical temperature gradient is described. The preferred temperature is found by determining calorimetrically the mean body temperature of fish in such a gradient. Preferred temperatures at various acclimation temperatures for a sample of young pumpkinseed, *Lepomis gibbosus*, are given.

MÜLLER, R., AND F. E. J. FRY. 1976. Preferred temperature of fish: a new method. J. Fish. Res. Board Can. 33: 1815–1817.

On décrit un appareil simple pour établir un gradient de température vertical, court et raide. La température de préférence d'un poisson est obtenue d'après la détermination calorimétrique de la température moyenne du corps du poisson dans ce gradient. On donne quelques températures de préférence en rapport à la température d'acclimation pour un groupe de jeunes crapets-soleil, *Lepomis gibbosus*.

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TEMPERATURE, among other factors, plays a major role in the distribution of fish in their environment. Fish tend to select a certain narrow temperature range if they have the choice to do so. This preferred temperature depends on the species of fish, as well as on its thermal history and factors like season, feeding, and age (for references see Coutant 1974). Often, the preferred temperature is determined in horizontal or vertical temperature gradients, in order to explain or predict the distribution of fish in a thermally changing environment. The preferred temperature of a fish is recorded according to its position in the gradient over a certain period of time. Such gradients are usually large and difficult to handle. Recent studies, for example, by Crawshaw and Hammel (1974) and McCauley and Huggins (1975) indicate that freshwater fish are capable of maintaining a fairly constant internal temperature close to the preferred temperature by moving back and forth in the gradient. As their body temperature represents an integration of all temperatures encountered, an attempt was made to determine the preferred temperature of fish in relation to acclimation temperature by measuring the mean body temperature. A short, steep vertical temperature gradient was employed.

Materials and methods — The test fish, young pumpkinseed (*Lepomis gibbosus*), weighed between 1.2 and 7.7 g. They had been collected in Ontario waters and were kept at a temperature of 7 ± 1 C for several months before the experiment began. The same group of initially 16 fish was successively acclimated to 8, 10, 15, 20, 25, and 30 C. Acclimation time was 1 day/C change followed by 1–2 wk at constant temperature. The daily light cycle was kept at a 12-h L:12-h D photoperiod throughout the test period from December to May.

The temperature gradient apparatus was made of

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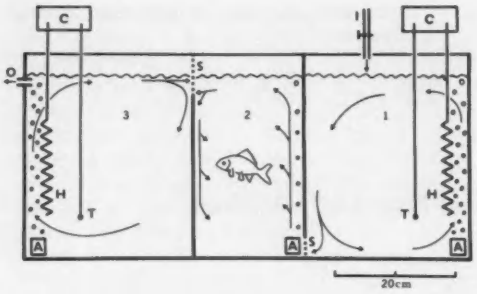

FIG. 1. Schematic drawing of temperature gradient apparatus. A, airstones; C, temperature controllers; H, heaters; I, water inlet; O, water outlet; S, screens; T, thermistors.

clear acrylic plastic sheet 6 mm thick and consisted of three chambers (Fig. 1). The overall dimensions of the original tank were 73 × 20 × 32 cm high. The test chamber itself was the central compartment, 18 × 20 × 32 cm high. Cold tap water entered the first chamber (1 in Fig. 1), at a rate of 0.4–0.6 liters/min. There the water was stirred by air and its temperature regulated at the lower temperature limit of the gradient before flowing into the test chamber through a screened inlet at the bottom of the wall separating chambers 1 and 2. Chambers 2 and 3 have a screened connection at the top of the wall separating them. The water in chamber 3 was maintained at the upper temperature limit of the gradient and stirred by vigorous aeration. Water passed to waste from the warm chamber through an overflow. As a result of the moderate turbulence caused by bubbles emerging from air stones in the two corners of the test chamber on the side adjacent to the cold chamber, the cold water on the bottom was gradually mixed with the warm water on the top. The intensity of this turbulence was crucial for establishing the temperature gradient and needed careful adjustment. Gradients ranged from 8 to 30 C for fish acclimated to 8 and 10 C, and from 14 to 38 C for the other ones. The temperature fluctuations at a given point were in the order of 0.5–3 C. As the gradient was built up by mixing two kinds of water saturated with air, the oxygen concentration at any point in the gradient was assumed to be near saturation too. Therefore, it was concluded that fish selected temperature, not oxygen. Two incandescent lights of 200 and 300 W at a distance of 1.5 cm to the side and above the apparatus illuminated the test chamber which was surrounded and covered by semitransparent dark green plastic sheet. Thus homogeneous subdued light conditions inside the test chamber were achieved.

Because of their small body size, two fish were usually put into the chamber simultaneously and measured together in order to improve the accuracy of the body temperature determination. After the fish had settled in the gradient for 40–120 min without any disturbance, they were quickly removed with a lift net and transferred to a calorimeter. The mean

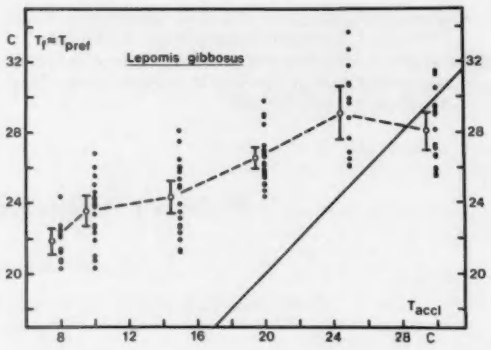

FIG. 2. Preferred temperature of pumpkinseed (*Lepomis gibbosus*) in relation to acclimation temperature as determined by the mean body temperature T_f.

body temperature was determined calorimetrically according to the method described by Fahmy (1972). A caloric factor of 0.87 cal/°C and grams body weight were used for pumpkinseed.

Results and discussion — Figure 2 shows the preferred temperature of pumpkinseed in relation to acclimation temperature as determined by the method described above. The "final preferendum" (Fry 1947) of 28.5 C lies just within the value range given by Neill and Magnuson (1974) for field observations of large fish in a thermally polluted lake (28.5–32 C). However, it seems to be rather low as compared to the 31.5 C found by Anderson (1951). The cause of this discrepancy may lie in the test procedure. As the same fishes were used for successive tests they acquired a certain shyness due to an apparent dislike of the body temperature determination (cold shock). Towards the end of the test period the fish tended to take more and more time to rise from the bottom where they had stayed in the beginning of the tests.[2] It is therefore suggested that the same fish should not be used for more than three tests. Despite this, the results indicate that the method is useful for estimating the preferred temperature of fish if space and energy are limited. Data gathered by this method will not show less variability than those obtained by observation of fish in a gradient. However, they may be said to represent more clearly the individual variability in the behavior of fish if single fish are tested.

[2]W. H. Neill (personal communication) suggests a false screen bottom be first located at the acclimation temperature of the subjects and then lowered after the fish has become habituated to the chamber and the gradient.

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Proliferative Branchiitis due to *Tetraonchus rauschi* (Trematoda: Monogenea) in Captive Arctic Grayling (*Thymallus arcticus*)

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WOBESER, G., L. F. KRATT, R. J. F. SMITH, AND G. ACOMPANADO. 1976. Proliferative branchiitis due to *Tetraonchus rauschi* (Trematoda: Monogenea) in captive Arctic grayling (*Thymallus arcticus*). J. Fish. Res. Board Can. 33: 1817–1821.

The monogenetic trematode *Tetraonchus rauschi* was diagnosed as the cause of severe proliferative and inflammatory gill disease among captive Arctic grayling (*Thymallus arcticus*). Grayling captured from the wild had few flukes and very limited pathologic lesions when compared to captive fish.

WOBESER, G., L. F. KRATT, R. J. F. SMITH, AND G. ACOMPANADO. 1976. Proliferative branchiitis due to *Tetraonchus rauschi* (Trematoda: Monogenea) in captive Arctic grayling (*Thymallus arcticus*). J. Fish. Res. Board Can. 33: 1817–1821.

Nous avons identifié le trématode monogène *Tetraonchus rauschi* comme étant responsable d'une sérieuse prolifération et inflammation des branchies chez des ombres arctiques (*Thymallus arcticus*) en captivité. Les ombres capturés à l'état sauvage ont peu de douves et très peu de lésions pathologiques comparativement aux poissons gardés en captivité.

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MONOGENETIC trematodes are common ectoparasites of fish but members of only a few genera, notably *Gyrodactylus* and *Dactylogyrus*, have been reported to be pathogenic.

The purpose of this report is to document *Tetraonchus rauschi* as a pathogen for captive Arctic grayling (*Thymallus arcticus*) and to describe the pathologic lesions produced in response to this parasite.

Materials and methods — The fish upon which this report is based were from a group of grayling being maintained in the Department of Biology, University of Saskatchewan, for behavioral studies. The fish originated from the Fond-du-Lac River in northern Saskatchewan and had been held in Saskatoon for varying lengths of time. The fish were maintained in a large circular tank containing about 18,000 liters of water, and in smaller 400-liter recirculating aquaria (Living Stream, Toledo, Ohio) for experiments.

Between December 1974 and October 1975, 10 fish held in the smaller aquaria became moribund or died and were submitted to the Department of Veterinary Pathology for examination. A complete necropsy was performed, and material from the anterior kidney was routinely cultured for bacteria.

A variety of tissues were fixed in Bouin's fluid for histopathology. These tissues are postfixed in 70% ethanol, trimmed, processed routinely, sectioned at 6 μ, and stained with hematoxylin and eosin. Gill parasites collected at the time of necropsy were preserved in 70% ethanol, and identified by the use of a key (Hoffman 1970) and by comparing specimens with the original description of *T. rauschi* by Mizelle and Webb (1953). Specimens were sent to Dr L. Margolis, Pacific Biologic Station, Nanaimo, B.C., for confirmation of the identification.

In October 1975, seven adult grayling were captured by angling from the Fond-du-Lac River to determine the extent of infestation in wild fish. These fish were immediately killed, and the head with gills intact were fixed in individual containers of 10% neutral buffered formalin. After fixation the left operculum was removed and the four gill arches on the left were dissected free and examined under a binocular dissecting microscope (20×). Flukes visible on the surface of the filaments were counted, but the filaments were not separated to check for flukes lying between the filaments. The gills from the right were processed for histopathology and examined.

Eight adult grayling that had been held for 2 mo in a recirculating aquarium which was supplied with a continuous flow of fresh water were divided into two groups of four fish each and placed in separate recirculating aquaria. The water in the group I aquarium was held at about 6.8 C (5.7–8.0 C), while that in the group II aquarium was maintained at about 12.5 C (7.8–14.7 C). Only enough water was added to the group I aquarium to compensate for evaporation; however, a small continuous flow of water was inadvertently allowed to enter the group II aquarium so that limited water exchange occurred in this tank.

FIG. 1. Gill arch dissected free from an Arctic grayling (*Thymallus arcticus*) that had died spontaneously. Note large numbers of gill flukes and area of hemorrhage which represented a focal area of mycotic involvement (arrow). ×4.5

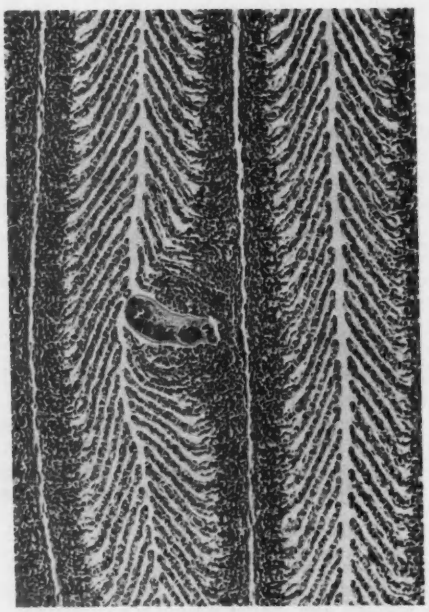

FIG. 2. Gill from lightly infested fish. Focal epithelial hyperplasia limited to area in direct association with embedded fluke. H & E ×65

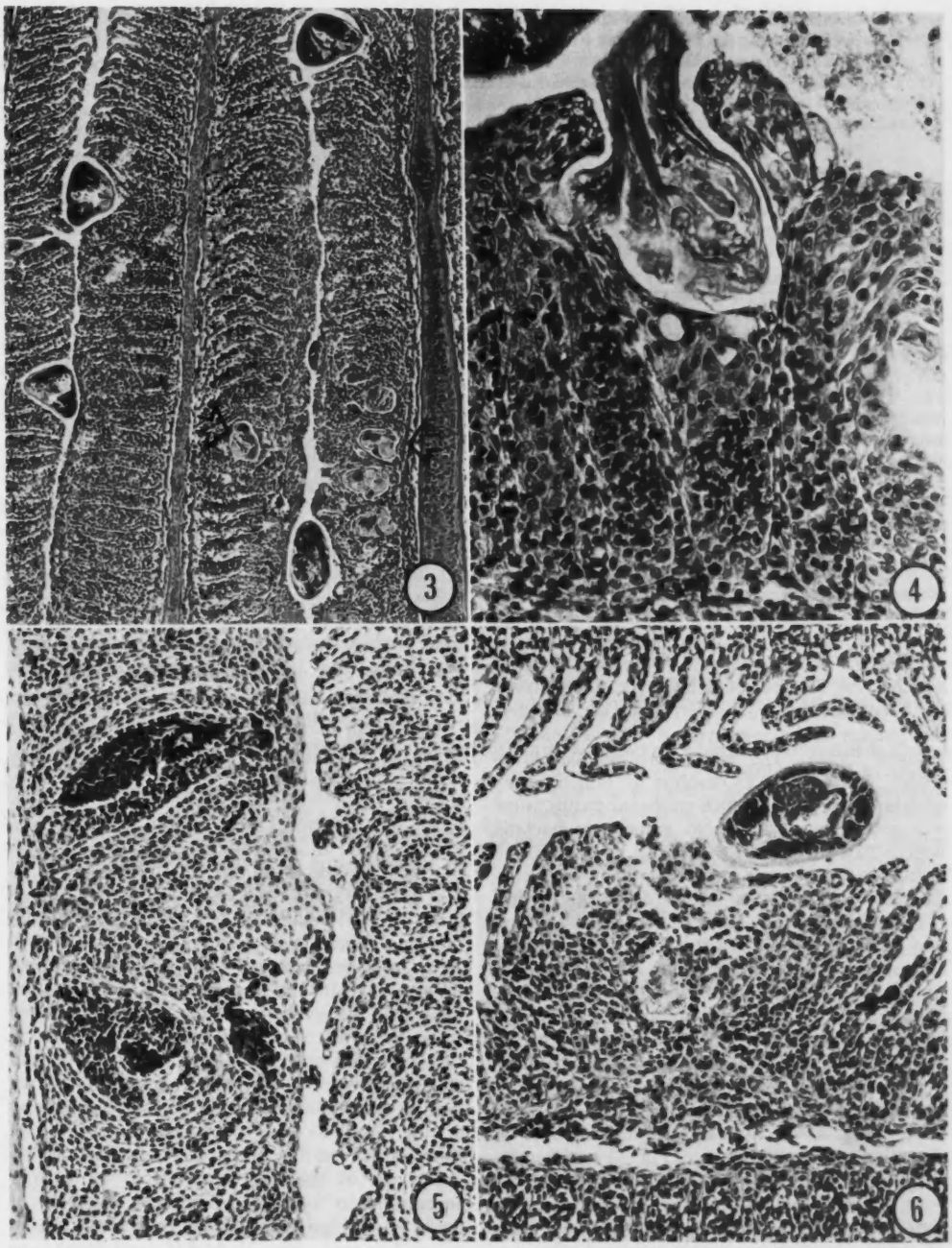

FIG. 3. Diffuse epithelial hyperplasia on gill in association with a large number of monogenetic flukes. Note embedded haptores (arrows). H & E ×85; FIG. 4. Epithelial hyperplasia on respiratory lamellae and interlamellar portion of filament in association with embedded haptore of fluke. Note large numbers of lymphocytes infiltrating area. H & E ×325; FIG. 5. Epithelial hyperplasia and ectasia of lamellar lacunae. H & E ×225; FIG. 6. Epithelial hyperplasia and hemorrhage in association with embedded haptore. H & E ×175

TABLE 1. Mean number of flukes on each gill arch of Arctic grayling (*Thymallus arcticus*) collected from the Fond-du-Lac River (wild fish) and maintained in aquaria at 6.8 C (group I) and 12.5 C (group II).

Group	No. of fish	Mean numbers of flukes			
		Gill arch 1	Gill arch 2	Gill arch 3	Gill arch 4
Wild fish	7	1.6	1.1	1.1	3.1
I	4	106.0	84.0	66.3	53.5
II	4	45.3	35.3	40.5	25.0

One fish from group I jumped from the tank on day 40 and was killed. Two of the remaining fish in this group died on day 41, and all the remaining fish were killed on this date. The heads of these fish were fixed in 10% formalin and examined in the same manner used for the wild fish.

Results — Ten grayling that had died spontaneously were examined, of which one fish was autolytic and another was considered to have died as the result of a traumatic injury. A consistent finding in the remaining eight fish was severe proliferative branchiitis in association with infestation by large numbers of monogenetic flukes (Fig. 1). These flukes were identified as *T. rauschi* Mizelle and Webb, 1953. Dr Margolis (Fisheries and Marine Service, Nanaimo, B.C.) confirmed the identification, but stated that he considers this species to be synonymous with *T. borealis* (Olsson 1893). The term "proliferative branchiitis" is used here to describe an inflammatory disease of the gills in which epithelial proliferation is a prominent feature. No pathogenic bacteria were isolated from any of the fish, and gross and histopathologic lesions in other organs were considered to be incidental to the death of the fish.

Histopathologically there was marked proliferation of the epithelium on the respiratory lamellae and on the interlammelar areas of the filaments. In the case of light infestations this was closely associated with attached trematodes (Fig. 2) while in many of the fish the epithelial hyperplasia was diffuse over the gill (Fig. 3). In addition to epithelial hyperplasia there were infiltrating lymphocytes in association with attached flukes (Fig. 4) as well as occasional ectasia or dilatation of lamellar lacuna (Fig. 5) and hemorrhage into the epithelium (Fig. 6).

In addition to the epithelial hyperplasia associated with flukes, two of the fish had focal areas of acute, necrotizing mycotic branchiitis. Apparently fungi had invaded distal portions of gills that had hyperplastic epithelium and produced a localized necrotizing reaction.

Four of the seven grayling collected from the Fond-du-Lac River had no visible flukes and the mean number of flukes on all fish was small (Table 1). There were no histopathologic lesions evident on these fish other than slight epithelial hyperplasia in direct association with flukes. In contrast, the fish in groups I and II were heavily infested when examined (Table 1), and there was severe epithelial hyperplasia diffusely over the surface of the gills of all of these fish except for one fish in group I which had relatively few flukes and focal epithelial hyperplasia only in direct association with attached flukes (Fig. 2). Both large and small flukes, some of which may have been larval forms, were evident on the gills of these fish.

Discussion — Williams (1967) reported that heavy infestations of monogenetic flukes may result under conditions of overcrowding, shallow stagnant water, and high environmental temperature, and Kearns (1968) held northern pike (*Esox lucius*) in small aquaria for several weeks to "build up the infection" of *T. monenteron* so that he might study the larval forms of this species. Khalil (1964) reported a rapid buildup of infestation by a species of *Macrogyrodactylus* on *Polypterus senegalus* captured from the wild and held in captivity. In the present case, grayling that likely had relatively few flukes when introduced from the wild developed heavy infestations in captivity. This occurred in fish held in both cold and warm water, but the effect of temperature on level of infestation could not be assessed because of the probable loss of free-swimming larval forms in the overflow from the group II aquarium.

Not all of the fish appeared to be equally susceptible to infestation since the numbers of flukes visible on the gills of individual fish in group I ranged from 31 to 851, and from 0 to 469 in fish in group II. The basis for this apparent "resistance" is unknown; however, Williams (1967) quoted several references reporting "im-

munity" of fish to reinfestation by monogenetic trematodes. Fluke infestation apparently did not become severe enough to become pathogenic among grayling maintained in a large outside pool, where the density of fish never exceeded 1 fish/1000 liters, but did among fish held in smaller aquaria where densities sometimes reached 1 fish/40 liters.

The gill lesions observed were similar to those described by others (Davis 1953; Molnar 1972; Bauer et al. 1973) except that the lamellar atrophy described by Molnar (1972) in chronic infestation was not seen. The fact that the one lightly infested fish in group I had only focal gill lesions in direct association with flukes indicated that the diffuse gill lesions seen in other fish were due to the flukes, and not to some other factor in the water.

A closely related species, *T. monenteron*, attaches to the host by impaling adjacent lamellae with two pairs of hamuli, and may withdraw the hamuli and move over the gills in a leech-like manner while feeding on gill epithelium (Kearn 1966, 1968). *Tetraonchus rauschi* appears to attach in a similar manner, and if this species also moves about during feeding, this may account for the diffuse hyperplastic response seen in many of the heavily infested fish.

The mycotic infection seen in two fish likely represented secondary infection superimposed upon gill damage caused by the flukes.

Restriction of fish to a small volume of water with limited or no water exchange maintains fluke ova and free-swimming larvae in close proximity to the host, facilitating reinfestation. This case illustrates that parasites or other agents that may not materially harm the host in a natural environment can become a serious problem among fish maintained under artificial conditions.

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PERSPECTIVES

Science for Canada's Fisheries Rehabilitation Needs[1]

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Abstract

LOFTUS, K. H. 1976. Science for Canada's fisheries rehabilitation needs. J. Fish. Res. Board Can. 33: 1822–1857.

A brief, generalized review of the current status of salmonid fisheries on the west and east coasts, and of selected representative waters in the freshwater area is presented. It is concluded that many fish communities and/or fish stocks are depressed, collapsed, or extinct as a result of severe stresses imposed directly, or indirectly, by man's activities. Rehabilitation of fish stocks and fish communities to levels approximating those of early years, and to levels capable of supporting more stable yields to meet growing client requirements appears practical. The need for explicit policy decisions with regard to sea ranching and rehabilitation as options for approaches to increasing fish abundance is stressed. Rehabilitation of stocks and communities will require additional science in areas such as hatching, rearing and selective breeding, fisheries engineering, and in the more precise definition of natural productive capacity of waters. Effective fisheries rehabilitation programs, and fisheries management generally, require: development of fisheries information systems; an adaptive or experimental approach; more social and economic data; synthesis and communication of science available; and fundamental reconsideration of the traditional institutional arrangements for fisheries work. Some important fisheries rehabilitation programs, carefully planned and assessed, can proceed immediately with confidence in their success; others must await improvement in water quality.

Résumé

LOFTUS, K. H. 1976. Science for Canada's fisheries rehabilitation needs. J. Fish. Res. Board Can. 33: 1822–1857.

L'auteur présente une brève revue généralisée de l'état actuel des pêcheries de salmonidés sur les côtes occidentale et orientale, et dans quelques nappes d'eau douce représentatives du domaine continental. Il en conclut que plusieurs communautés et/ou stocks de poissons sont affaiblis, affaissés ou éteints comme résultat des sérieuses contraintes imposées directement ou indirectement par les activités humaines. Il semble pratique de réhabiliter les stocks et les communautés ichtyologiques à des niveaux se rapprochant de ceux des années précédentes et à des niveaux capables de fournir des rendements plus stables de façon à pouvoir satisfaire une demande accrue de la part des clients. On insiste sur le besoin d'une décision explicite sur le choix entre l'élevage en mer et la réhabilitation comme moyens d'augmenter l'abondance du poisson. La réhabilitation des stocks et des communautés nécessitera plus d'effort scientifique dans des domaines tels que pisciculture, élevage, croisements sélectifs, génie des pêches, de même qu'une définition plus précise de la capacité de production naturelle des eaux. Des programmes efficaces de réhabilitation des pêches et de gestion en général requièrent des systèmes d'information; une approche adaptive ou expérimentale; plus de données sociales et économiques; des moyens de synthétiser et de communiquer les résultats de la science; et une reconsidération fondamentale de l'organisation traditionnelle des institutions œuvrant au domaine des pêches. Quelques programmes importants de réhabilitation des pêches, planifiés et évalués avec soin, peuvent être mis à exécution dès maintenant, en toute confiance quant à leur succès; d'autres devront attendre que soit améliorée la qualité de l'eau.

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Introduction

A broad overview of the major issues confronting Canadian fisheries scientists was presented by Regier and McCracken (1975) as a framework within which to discuss the science needed in the management of Canada's shelf-seas fisheries. That overview is also a useful introduction to this perspective of the science needed for fisheries rehabilitation. Explicit recognition of rehabilitation as a major thrust within the new approach to fisheries management seems necessary.

To develop this perspective on the science needs for fisheries rehabilitation, the author briefly reviewed the current status of selected stocks and fish communities and attempted to assemble best judgments about the causes for their depressed states. The first half of this report presents the reviews for salmon stocks, with emphasis on west coast salmons, and for freshwater fish communities with emphasis on the Great Lakes. These selections are presented as examples thought to be representative of what has happened, and what is continuing to happen, to fish communities across the country.

This perspective takes it for granted that fisheries rehabilitation is appropriate and does not

enter that discussion. For Pacific salmon the case for rehabilitation appears to have been made (Larkin 1975), at least from the fisheries point of view. In the Great Lakes the current program of sea lamprey control, an integral component of a rehabilitation program, attests to the fact that this case has also been justified.

Because water quality considerations in many instances are prerequisite to fisheries rehabilitation programs, it has been difficult to entirely avoid straying to that topic which is the subject of a separate study in this series.

Stories of Some Important Fisheries

On the West Coast

Exploitation of salmonids on the west coast by commercial fishermen began on the Fraser River sockeye in the mid-1800s. Small boats, using sails for power and gillnets as gear, worked in or very close to the river and their harvest was salted in barrels for export. The development of the hermetically sealed can in 1870, and the arrival of power boats in the 1920s were events of major significance in the growth of the industry. By the end of the 1920 decade all five salmon species were being exploited and some of the more readily accessible stocks were being overfished. A purse-seine fishery for pinks and chums, and a troll fishery for coho and chinook emerged in addition to the gillnet fishery for sockeye. Fishermen were quick to identify the catching gear most appropriate to the characteristics of the various species. The concentrations of salmon associated with their homing at spawning time, particularly precise in the sockeye, have rendered them highly vulnerable to overexploitation. Management techniques have, therefore, tended to concentrate on arrangements to provide for adequate escapement of spawners to the rivers. In very general terms the stocks from most rivers are mixed at sea and it is not presently possible to selectively fish any one stock. As the stocks move in and along shore with the approach of spawning season, segregation is progressive in both time and space, becoming essentially complete only at the appropriate river mouth. Inshore lines, within which fishing is prohibited, have been established on the basis of average migration routes, and salmon which arrive inshore of these lines constitute the "spawning-escapement." An offshore line, outside of which no salmon fishing is allowed (except by trollers for coho and chinook), precludes the harvests of stocks when they are still actively growing and when they are intermingled. These two lines and a tightly controlled fishing season improve the opportunity for controlled and selective exploitation of the salmon as they move inshore and segregate in approaching their natal streams.

Since about 1950, technological improvements in the commercial industry have sharply increased the fishing power even in the face of license limitations. The response by management generally has been to increase the sanctuary areas, and to reduce the number of days and/or hours when fishing is permitted. During this recent period also the recreational fisherman has emerged as a significant "client," particularly for coho and chinook stocks.

The stock concept, long implicit in the statements and recommendations of managers and research people, has become explicit (Ricker 1972) thereby placing on management the responsibility for a degree of finely tuned, stock-by-stock control that is essentially an order of magnitude beyond which they and the industry have become accustomed.

During the period of fishery development, other events significant to salmon abundance have "progressed" apace. Forest industry operations have included small dam construction and extensive road building in addition to the obvious prime target of tree removal. As a result some stocks have been denied access to their "home" tributary and others have suffered poorer reproductive success by virtue of sedimentation and/or modified stream flow patterns. Mining developments have had similar impacts. Hydro electric power developments in many instances have modified stream and river flow patterns and major dams and diversions have eliminated some major runs. The salmon vs. power story in the northwestern United States is particularly vivid. There, as a result of having lost most of the productive capacity of freshwater nursery areas, agencies have opted for the "sea ranching" as opposed to "rehabilitation" approach to increasing salmon stocks. The present level of pollution of municipal and industrial origin in the Fraser River estuary must now be a matter of serious concern.

The event which became famous in salmon literature as "Hell's Gate" has now been largely removed and/or circumvented and most, if not all, stocks which it temporarily barred from their spawning grounds have been reestablished. A serious slide on the Babine River in the early 1950s caused a decline of Skeena River stocks, but prompt action has provided for reestablishing the runs. Many less spectacular, but similar slides have occurred elsewhere but corrective measures have not been effected to date.

The net result of the foregoing kinds of development has been an average total commercial salmon catch for the period 1962–71 of about 150 million pounds. Ricker (1962) suggested that west coast waters have the potential of producing about double the current production level: 300 million pounds. Harvests in the early 1900s were probably of that order of magnitude.

Sockeye — Sockeye (*Oncorhyncus nerka*) was the first of the Pacific salmon species to be heavily exploited because of its availability at the Fraser, and because of its high value as a canned product. The average catch of sockeye from the Fraser River alone during the 16 years prior to the Hell's Gate slide in 1913 was in the order of 70 million pounds. Much of the rock was removed from Hell's Gate by 1915 permitting the renewed ascent of a number of stocks. Fishways, completed in 1946 by the International Pacific Salmon Fisheries Commission, provided further correction to the obstruction and additional stocks, particularly early and midseason runs, became reestablished over several years. Some stocks are thought to have been lost as a result of the slide, and several have yet to completely recover (Ricker 1972). Current annual sockeye harvests are well below half the original harvest levels.

Other important sockeye-producing river systems include Smith Inlet, Rivers Inlet, Skeena, and Naas. Smaller runs are scattered along the mainland and around Vancouver Island. Most stocks have recently been providing harvests amounting to no more than half of earlier harvest levels.

Sockeye mature mainly in their fourth year in southern British Columbia and in either their fourth or fifth year in central and northern regions. Typically, incubation takes place in stream situations and the fry move to "nursery" lakes for the first year, before moving downstream for 2 to 4 years in the ocean.

In the Fraser River, estimates of the numbers of spawners in important streams have been recorded annually by the B.C. Department of Fisheries, by the Canada Department of Fisheries, and most recently by the International Pacific Salmon Fisheries Commission. Originally upwards of 40 stocks of sockeye used the river and were reared in lakes from Coquitlam and Pitt near tidewater to Takla at the head of the Nechako–Stuart system. Ricker (1972) states, "Some stocks have been exterminated by power and other dams (Coquitlam, Alouette), some disappeared following the obstruction of the river by rock slides in 1913–14 (Salmon River, Eagle River, Upper Adams River) and one (Chilliwack Lake) has not been reported since 1935 and may no longer exist." Killick (1955) described the migration times of a number of the major Fraser stocks in some detail. Various other authors' works describing morphological differences between stocks are reviewed by Ricker (1972).

Skeena River sockeye include at least 20 stocks even though there is only one major nursery lake in the system. There are scattered references in other literature and in project proposals which make it clear that discrete stocks are characteristic of sockeye wherever they occur.

The available documentation strongly indicates that at the turn of the century, when stocks of sockeye were at substantially higher levels than they are now, many discrete stocks were present. Some stocks are known to have been lost; others persist, but at much reduced levels. It is not certain how many stocks are involved in these categories because the records of stock identity were established only relatively recently. It is also recognized that some "nursery" lakes are carrying fewer young salmon than they are capable of rearing. These two facts and the general life history characteristics of the species prescribe the science needed for rehabilitation. We need to be confident that we know the rearing capacity of the nursery lakes. The available or potentially available capacity of the nursery lakes can be used to produce more smolts. To use this capacity, fry production needs to be increased, preferably by reestablishing stocks which have been lost, by rehabilitating stocks that are at low levels, and/or establishing spawning channels to increase the fry production from runs which now use the lake for rearing. The latter alternative is likely the least certain method, though possibly the most appealing, because it assumes that any kind of fry will do the job. Except in cases where natural barriers were and continue to be the factor limiting reproduction, and hence full utilization of nursery lakes, it seems likely that in the long term the surest bet is that of reestablishing the stocks which evolved earlier.

Pink — Pink salmon (*Oncorhynchus gorbuscha*) came under direct exploitation at the Fraser River as an alternative to the up-river sockeye stocks that collapsed as a consequence of the Hell's Gate slides. Production of pinks was as high as 110 million pounds in 1917 and averaged about 70 million pounds in the first few cycle years following 1913. These pink stocks, affected by the slide and by heavy exploitation, declined in the 1920s to about half their earlier abundance levels and the industry

moved north to intercept other runs. In these new waters the even year runs provided an average of 80 million pounds for several years. Total catches of pinks during the 1960 decade averaged about 60 million pounds per year, reflecting some overall improvement from slightly lower catches during the 1940 and 1950 decades. Ricker (1962) suggests that the average catches have been achieved partly by the fishing-up process, and that many stocks have been considerably depressed. Ricker (1962) and other west coast salmon workers recently (R. McLeod, personal communication) feel that pink harvests could be doubled to at least 100 million pounds per year by more intensive management and by successful rehabilitation projects.

The up-river pink stocks in the Fraser have not yet fully recovered from the effects of the Hell's Gate slides, and some down-river stocks have been depressed by the combined effects of exploitation, siltation, dredging, and by modified stream flow patterns. Some northern stocks are depressed for some of the same reasons. There is also optimism that significant "off-year" runs of pinks can be established in the Fraser River and in the Queen Charlotte Islands runs.

Pink salmon mature in their second year and, at maturity, they average about 5 pounds in the southern and about 4 pounds in the northern part of British Columbia. The Fraser and other southern streams, have dominant runs in odd-numbered years. Most Queen Charlotte Islands streams have dominant runs in even-numbered years, odd-numbered years having very few pinks. In most other regions, there seems to be no pronounced pattern of dominance during one set of years over the other. Pinks spawn in appropriate stream situations which may occur in the intertidal zone, in downstream tributaries such as the Chilliwack and Harrison Rivers (IPSFC 1972), or in the larger streams such as the Fraser and Thompson rivers several hundred miles upstream. The young move downstream to saltwater as fry. There is ample evidence that the stock concept, thoroughly documented for sockeye, is also characteristic of pinks (Ricker 1972).

"The environmental factors apparently influencing the production of Fraser River pink salmon have been discussed in the 1967 and 1969 Annual Reports of the International Pacific Salmon Fisheries Commission. Natural variations in the environment at the spawning grounds during the period from spawning to emergence of fry have resulted in survival from eggs to fry ranging from 9.2 to 18.4%. Variations in environment during the remainder of the life cycle to returning adults have resulted in yields ranging from 1.14 fish to 10.70 fish per spawner. The data indicate a relatively stable environment at the spawning ground, and a relatively variable environment in the estuarial and marine rearing areas." (IPSFC 1972, p. 70)

Rehabilitation opportunities may be realized by: (a) improving spawning and incubation facilities for those runs that have suffered from siltation, dredging, and water flow irregularities (stream flow stabilization is most important), (b) expediting the reestablishment of runs depressed by events such as the slides at Hell's Gate, and (c) establishing off-year runs. Protection of water quality in the streams and estuaries and careful control of adequate spawning escapement are also prerequisites for rehabilitation.

Chum — It was not until the late 1920s that chum salmon (*Oncorhynchus keta*) were fished actively. Catches in the order of 70 million pounds were recorded for several years. Although this species has traditionally been of low economic value, recent changes appear to indicate a substantially higher value in the near future (F. Fraser, personal communication). Harvests have fluctuated considerably for many years, probably reflecting demand more than supply, and average annual harvests over the past decade have been in the order of 20 million pounds.

The spawning, incubation, and rearing needs for chums in fresh water are quite similar to those for pinks. Although the chums of the Yukon River move as far upstream as Teslin Lake, a distance of 2700 km (Gilbert and O'Malley 1921), generally chum stocks spawn downstream, relative to pinks. Very few spawning chums reach Babine Lake on the Skeena for example, and in the Fraser they rarely pass Hell's Gate (Ricker 1972). Young chum salmon make little or no demand on the stream habitat for food because, like pinks, they move to the estuaries at an early age. Their sea life, however, is much longer than that for pinks, usually maturing in their fifth year and at an average size of about 12 pounds. As in the sockeye, the chum salmon appears to be characterized by discrete stocks.

Opportunities for rehabilitating chum stocks are of the same general types as those suggested for pinks, except that there is no "off-year run" opportunity.

Coho — Extensive commercial fishing for coho salmon (*Oncorhynchus kisutch*) was established by the mid-1930s. Trolling developed early as the principal harvest method and remains so today, although some coho are taken by gillnets

and seines. The total commercial harvest, averaging about 25 million pounds, was relatively constant until about 1960 when a decline became evident. That relatively constant yield may have been a result of a fishing-up process on successive stocks (Ricker 1962), and was probably more apparent than real. During the 1960s and 1970s a recreational fishery has emerged in the Strait of Georgia and it now harvests in excess of 1 million pounds annually. Though sockeye have been for many years the most highly valued commercial species on a per-pound basis, coho have recently become equally, or slightly more, valuable. This increased commercial value, together with the substantially higher values on a per-pound basis usually attributed to sport-caught fish, create a high demand situation.

Spawning runs of coho enter most major river systems used by other salmon species, but they are somewhat unique in that they also use a great many small coastal streams and up-river tributaries of large rivers. Spawning and incubation requirements are generally similar to those of sockeye in that they spend a year after hatching in fresh water before going to sea as smolts. Unlike the sockeye, however, the freshwater period is usually spent in flowing water rather than in nursery lakes. In general they mature and return to spawn in the latter part of their third growing season as 7–8 pound fish.

The foregoing life history characteristics make the coho more susceptible than other salmon species to the stresses imposed by the extension of man's activities. Almost any alternative use of water, even in very small streams, has the effect of reducing coho smolt rearing capacity. Dams and diversions have had substantial effects on stocks using rivers such as Chekamus, Capilano, Coquitlam, Cowichan, Puntledge, and others (Ricker 1962). Summer flows have been modified by logging and agricultural practices and this effect, with sedimentation, has reduced the capacity of the streams to rear coho. Urban development, mining, and local use of DDT in forest spraying have also had impact on coho.

Enhancement opportunities for coho include (a) the construction of fishways to provide spawning coho access to upstream rearing areas which they are unable to reach because of natural barriers, or because of newly installed engineering works; (b) installation of flow-control structures to stabilize summer flows at higher than present levels; (c) use of extensive fish culture facilities (hatching and rearing to the smolt stage) to replace lost stream rearing capacity. It has also been suggested that increased poundage, if not numbers, of coho could be achieved by management arrangements that would delay the harvest of maturing coho.

Chinook — Chinook salmon (*Oncorhynchus tshawytscha*) became a regular part of the commercial salmon harvest in the 1930s at about the same time as coho. Catches have been relatively stable at about 15 million pounds annually until recently when a decline has become evident. Again the earlier relatively steady yields may have been more apparent than real by virtue of the fishing-up process. Recent landings are characterized by a reduced catch-per-unit effort and by fish of smaller size in the catch. A significant recreational fishery is now emerging for chinook similar in extent and location to that for coho.

Some chinook stocks have either been exterminated or are at precarious levels at the present time: Nechako and Bridge River stocks on the Fraser (Ricker 1972) and the Pungledge River stocks (Ricker 1962).

Spawning runs of chinook are much less numerous than coho in that they use only medium and large river systems. Some of the largest runs in the United States (the San Joachim, Sacramento, Klamath, and Columbia River stocks) have been decimated or completely lost as a result of industrial developments, principally dam construction. The ample literature concerning these stocks, and to a lesser extent reports based on British Columbia stocks, demonstrates that chinook populations are made up of many discrete stocks. Spawning runs tend to be widely separated seasonally.

In general the demands made on the stream system by chinook are intermediate between those made by coho on the one hand, and by pinks and chums on the other. Characteristically, young chinook remain in the streams, feeding actively for several weeks before moving to the estuaries during summer or early autumn. Most chinook mature during their third growing season at sea and return at sizes ranging up to 60 pounds or more. Some mature and return during their second growing season and are known as "jack springs."

Enhancement opportunities for chinook include (a) construction of fishways to provide access to upstream spawning and rearing areas which are not now available because of natural or man-made barriers; (b) installation of flow-control structures as for coho; (c) use of fish culture facilities suitable for rearing to the advanced fingerling stage, essentially a substitution for the natural stream environment.

Steelhead — The native range of steelhead (*Salmo gairdneri*) is similar to that for salmon:

most streams used by spawning salmon are also used by spawning steelheads. In some larger watersheds there have developed stocks of rainbow trout which complete their life cycle in fresh water, substituting lakes for the sea during their postsmolting years of major growth. The popularity of the species among anglers, and its relatively easy culture and modest water quality demands, has led to its introduction to many areas outside its native range (MacCrimmon 1971). Almost all introductions that have become self-sustaining (e.g. Great Lakes), complete their life cycle in fresh water.

Beginning in the early 1800s, steelheads were fished commercially in U.S. coastal waters (Sheppard 1972). A harvest exceeding 8 million pounds was recorded in 1895 and annual catches of 4 million pounds were common until the mid 1920s. Since then commercial catches have declined, by virtue of lack of availability and because of legislative restrictions, to about 600,000 pounds in 1969. The steelhead is now considered a "game" fish and commercial harvest figures represent incidental catches by salmon fishermen and by native people as prescribed by treaty rights.

In British Columbia steelhead are taken by commercial salmon fishermen incidentally. The largest catches are taken by gillnet fishermen in the estuaries of the Skeena, Naas, Bella Coola, and Fraser rivers. An approximate average of 20,000 steelhead per year has been estimated as the total incidental catch for B.C. waters, 90% taken in gillnets, the remainder by trolls and purse seines (Withler 1972). Few good data are available on the extent of the Indian food fishery in B.C. but Withler (1972) considers that the number involved are likely less than 10,000 per year.

The tremendous growth of the recreational fishery for steelhead in the U.S. has been matched by a more modest but significant sports fishery in B.C. Withler (1972) assembled data from a number of sources to indicate the extent of this fishery, and to discuss the economic and social questions which are emerging in the efforts to meet angler demands.

Steelhead spawn in streams early in the year, January–June, depending upon the stock. The fry live and grow in small streams, larger rivers, or lakes for various periods up to 5 years (Narver 1969; Narver and Withler 1971). Upon reaching an appropriate size there is a "smolting," usually in the spring, and a movement to salt water. The life at sea is characterized by active feeding, rapid growth, and considerable travel (Turner and Aro 1968). The length of life at sea may vary from a few months to 4 years (Shapovalov and Taft 1954; Narver and Withler 1971) and the fish exhibit a strong tendency to return to natal streams at spawning time. In general, two types of steelheads, "summer" and "winter," are recognized, according to the season when they enter the rivers. Summer steelhead are immature sexually when they enter, usually between May and September, and spawn as much as 8 months later, usually in the upper reaches of the watershed. Winter steelhead enter the rivers fully mature during November through April and tend to spawn in the lower portions of the watershed. The stocks maintain separation during spawning (Smith 1968) though both may be present and spawning at the same time.

The life history characteristics of steelhead are such that stocks have been subjected to the same stresses that have depressed salmon stocks. Thus the construction of dams, the impacts of the forest, mining, and agricultural industries have in some cases eliminated stocks, and in others have reduced stocks to critically low levels. Although steelhead have not been a target species in commercial fisheries, their incidental capture by salmon fisheries is reasonably well documented. It is anticipated that successful salmon rehabilitation, in providing increased fishing opportunities for salmon fisheries, may well result in larger total incidental catches of steelhead. Whether or not there will be real competition between the growing number of recreational fishermen and the commercial fisheries is not known. It is inevitable, however, that competition will be "apparent" from the recreational anglers point of view, particularly in areas adjacent to population centers, where stocks will tend to be at low levels for other reasons.

In the U.S. intensive work directed at rebuilding and/or replacing stocks of steelhead to meet the demands of the recreational fishery has given rise to an extensive fish culture program. Best results have been realized from culturing the fish to the smolt stage and releasing them at carefully selected times and places. Wagner (1967) reports details of the cost of the program per fish creeled. One problem associated with this sort of approach to the provision of angling opportunities is the tendency to concentrate on a few locations for reasons of economy, and to produce an artificial concentration of opportunities and of anglers, in both time and space. There is considerable doubt that this is the kind of fishing opportunitiy sought by most anglers (Haig-Brown 1959; Pearse Bowden Economic Consultants Ltd. 1970, 1971).

In looking toward intensive management of

B.C. steelhead stocks, Withler (1972) documents the following science needs:

> "I. The most urgent need is for fishery managers to become aware of what steelhead anglers really want when they go fishing, while at the same time anglers must become aware of the constraints which may stand in the way of satisfying their wants.
> "II. There is an urgent need to inventory and describe the province's steelhead stocks. First priority should be given to those which are endangered by immediate industrial or domestic development, to major stocks, and to those in high angling-demand areas.
> "III. There is a need to develop methods of improving steelhead production in natural streams.
> "IV. There is a need to discover the most effective and economical methods for producing steelhead by artificial means, adapted to the special conditions of British Columbia.
> "V. There is a need to know, before major plantings from hatcheries and/or transfers between streams are made, whether or not natural stocks are likely to be endangered by introduction of disease or by genetic pollution."

Most of the above suggested needs are parallel to those for various species of salmon. It is evident that there is much commonality in science needs, but much risk to species, to stocks within species, and to the needs of different client groups if rehabilitations projects are approached on other than a community of species basis.

On the East Coast

Man's activities began to have impact on east coast fisheries resources about a century earlier than on the west coast. These activities have included exploitation of the fish stocks, agriculture, forestry, mining, and power development. Development of these activities appears to have occurred at a more leisurely pace on the east coast than elsewhere in Canada and the responses in the fish stocks to the stresses imposed tend to have been more gradual, at least until recently, and to have attracted less attention. Regier and McCracken (1975) have provided an overview, with particular reference to exploitation, of events in the shelf-sea fishery. McCracken and MacDonald (1976) provided a perspective of the inshore fisheries giving special emphasis to social and economic considerations. Both studies contain information pertinent to anadromous stocks, Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*), which are briefly discussed here.

The physiography of the east coast of Canada is such that the rivers tend to be shorter and smaller than on the west coast. The anadromous fish stocks that have evolved in this situation have always been less abundant, and more diffuse in character than has been the case on the west coast. Perhaps because of this diffuse character, and perhaps also because of tradition and the more ready access to other fish stocks, fisheries that have developed on the east coast have tended to concentrate attention on stocks other than the anadromous species. This seems to have been in contrast with the west coast situation where the salmons constituted the resource central to fisheries development. In rivers, the Atlantic salmon to a major extent was reserved for the "gentleman" angler by virtue of the stream leasing technique of management, hence, although the small group which did have access to stream angling have been both vocal and constructive in their concern for effective salmon management, there seems not to have been a broad base of concern among provincial residents. Again, unlike the west coast events, there has been no "Hell's Gate" disaster, with its consequent spectacular impact on the resource, to focus concerned attention. In recent decades attention has been more sharply focused on these anadromous stocks by events such as awareness of heavy metals contamination downstream from accelerated mining operations, extensive insecticide spraying operations by the forest industries, by the intensification of exploitation on the salmon stocks off Greenland and around Newfoundland, and by hydroelectric developments.

Atlantic salmon — The general features of the life history and ecology of Atlantic salmon have been recorded by naturalists and by fisheries workers in Europe and eastern Canada for well over a century. During the first half of the current century much additional useful detail has been published. Elson and Kerswill (1968) drafted an excellent review of such information and suggested avenues for further research. Very generally, spawning is in the fall of the year in the upper reaches of streams and the young fish spend two or more years in the stream habitat before smolting and descending to the sea. One or more years of sea life characterized by active feeding, considerable travel, and extensive growth is usual before returning to "home" streams and spawning. There is substantial evidence to indicate the "stock concept," explicitly identified as operative in west coast salmonids, is also a fact in Atlantic salmon.

The current depressed status of Atlantic salmon

stocks has been discussed by McKernan (1972) and Needler (1972) both of whom present broad historical and international perspectives. In the same symposium Power (1972) presents his overview of salmon management to the present, and all three authors make a strong case for new initiatives to rehabilitate the resource.

Exploitation of salmon, following the most recent event in the fishing-up process off Greenland, which may have cut deeply into the remaining stocks, has now been sharply curtailed. For the past several years commercial fishing has been banned in Port au Basques and off the Saint John, Resitgouche, and Mirimachi rivers to allow recovery of depressed stocks in those areas. When stocks are rebuilt to levels that can again sustain limited exploitation, it is likely that the pattern of fishing permitted should recognize the stock concept, and the need to fish separate stocks inshore after they have segregated.

The other major stresses which have been identified as having serious impacts on salmon stocks relate to both quality and quantity of habitat in the freshwater area. Elson et al. (1972) present a review of the effects of chemical pollutants on east coast salmon and suggest that both the health of the fish and the productive capacity of the streams have been impaired. Huntsman (1972), Needler (1972), and Stewart (1972) review and confirm the well-known relationship among stream flow characteristics, in-stream salmon movements, and stream productive capacity, and they stress the need to effectively circumvent both natural and man-made obstructions. Collectively the stresses impacting salmon stocks in fresh water appear to have severely depressed most of them and have impaired the productive capacity of the rearing habitat to well below the potential described by Kerswill (1967), Mills (1972), and Gibson (1972).

Rehabilitation of Atlantic salmon stocks appears to be an objective endorsed by all concerned. Much of the science that would be necessary is now available, and it would seem feasible to more than double the present abundance level, given effective application. The diffuse nature of the resource and the traditional use patterns may present unique social and economic concerns, but given new institutional arrangements involving a broader segment of the public, together with the already well-established special value of salmon, there should not be insurmountable constraints.

Exploitation has already been reduced in some areas. The impact of chemical pollution has been documented and although controls are being applied the effort requires intensification. Fish culture facilities are in need of modernization to provide for full application of the science presently available. Initiatives to modernize engineering facilities such as fishways and flow-control devices, and to undertake stream habitat improvement appear necessary.

Brook trout — The extensive studies of White (1940), Elson (1940), Smith (1948; 1951; 1952; 1960; 1963; 1968), Smith and Saunders (1967; 1968) and Saunders and Smith (1962a, b) have documented the life history, ecology, and management of brook trout on the east coast. Most studies were undertaken on Prince Edward Island waters and on a few other maritime streams in conjunction with salmon studies. It is difficult to compare the present status of the anadromous brook trout resource with its status in earlier years. One would expect that the stresses imposed by agricultural, mining, forestry, and power developments would have acted to depress brook trout stocks much as they have salmon stocks, but documentation of such effects has not been pursued. On Prince Edward Island it seems that although the number of "sea-run" trout may have been reduced by small dam construction, the overall availability of brook trout to anglers has not been reduced either by the dams or by agricultural runoff.

Brook trout is included in this perspective, not in detail but simply to provide for consideration of two points: (1) the apparent contrast in responses to man's impact by brook trout and Atlantic salmon, and (2) the value of relatively unsophisticated stream habitat improvement techniques in increasing the productive capacity of streams.

In the Freshwater Area

There is no single reference available which gives a summary of the limnology of Canadian lakes and of their fish communties as they were before development imposed changes. Such base line documents could and should be developed from the many historical and early scientific records that exist in scattered bits and pieces. They would provide excellent perspectives for use in fisheries management generally, and, more particularly, for use in establishing objectives for fisheries rehabilitation initiatives.

The general limnology of 12 Canadian oligotrophic lakes and their fish communities, as they probably existed prior to the impacts of man, were described by Ryder (1972). He also summarized the relative degree of environmental change imposed by man's activities in each lake.

It seems unlikely that additional examples of oligotrophic lakes would add much of substance to the generalities which emerged in that paper. While it seems probable that similar syntheses of information for other categories of lakes (mesotrophic and eutrophic) would yield generalities differing only in detail, the benefits from undertaking such syntheses would be substantial.

The SCOL symposium (Loftus and Regier 1972) represents a synthesis of information available on the limnology and of the fish communities of 12 oligotrophic Canadian lakes and a number of similar European lakes. That synthesis was presented within the framework of examining the impact of major man-induced stresses, exploitation, cultural eutrophication, and species introductions on the fish communities over time. These lake and fish community "case histories" constituted "trend-through-time" data series and their comparison allowed a more confident perspective on cause and effect between major stresses and fish community response than had hitherto been available to fisheries workers. As such they provide a kind of perspective necessary to consideration of rehabilitation programs. Some case histories are discussed below, along with some other waters and fish communities. These are thought to be representative of the kinds of events that have occurred, or are occurring in many if not all Canadian fresh waters, and, therefore, indicate the kinds of fisheries rehabilitation science required throughout the freshwater area.

Lake Superior — A general review of current knowledge of Lake Superior and its fish stocks was reported by Lawrie and Rahrer (1972; 1973). Large, deep, and cold, Lake Superior is highly oligotrophic and relatively unproductive. All species of historical importance to the commercial and/or recreational fisheries are now seriously depressed in comparison to former abundance levels (Great Lakes Fishery Commission). Some stocks of lake trout, particularly those discrete inshore spawning populations, some of which were identified by Loftus (1958), have disappeared.

From a water quality point of view, Lake Superior apparently remains healthy, at least relative to the present condition of the other Great Lakes. Lawrie and Rahrer (1972) suggest that sawdust and other woody materials added to the tributaries and some shallow-water benthic areas from logging and associated operations beginning in the last century, probably contributed to the depression or disappearance of some stocks of species such as lake sturgeon and lake whitefish. While the practices which contributed these materials to the lake have changed in recent years, Ryder and Johnson (1972) suggest that their depressing effect is likely to be long-term in nature. Presently, water quality is acceptable for fish except in local situations where municipal or industrial effluents have been discharged. The loss of one walleye stock in Nipigon Bay in recent years was attributed to an industrial effluent (Ryder 1968).

Overexploitation is believed to have been a factor in the decline of every major species in Lake Superior, at least at some stage. Lawrie and Rahrer (1972) reached this conclusion despite their discomfort with some of the data series available. They also provide an illuminating account of the fishing-up process as it must have occurred on Lake Superior stocks, particularly lake trout, and of how the evidence of overexploitation was obscured until recently. The annual reported landing of lake trout averaging about 5 million pounds from the late 1800s through 1950 were apparently maintained to an important extent by the fishing-up process. The additional exploitation from predation by expanding sea lamprey populations in the early 1950s brought about a sharp decline in lake trout abundance by 1962, when the landings fell to well below a half million pounds. A major international effort by the Great Lakes Fishery Commission in sea lamprey control has resulted in a reduction in lamprey abundance by some 90% from their peak. A lake-wide program of lake trout rehabilitation has achieved plantings of hatchery-reared yearling lake trout in the order of 2 to 3 million annually since 1960. Results from these plantings, while encouraging, are somewhat below expectations. Lake trout numbers in some locations have reached levels comparable to those of prelamprey years (Pycha and King 1975). In other areas, however, the former abundance levels remain as distant targets. The offshore stocks, those least affected by sea lamprey predation, are reproducing well, and their age structure and abundance can probably be manipulated by finely tuning the level of exploitation. The inshore stocks, those most severely damaged by sea lamprey predation, have received virtually all the rehabilitation effort. There is now widespread evidence of limited reproduction by the planted stocks, but in general the age structure and mortality of the stocks in the lake are such that only a few fish are reaching maturity, and by present apparent rates of increase, the target of naturally reproducing lake trout stocks is some years away. Concern is being expressed about (a) the adequacy of the level of sea lamprey control, (b)

the planting techniques, (c) the impact of exploitation on planted stocks, (d) the adequacy of numbers planted, particularly on the Canadian side, and (e) the genetics and/or health of fish planted, particularly with reference to the former structure of the lake trout population, which was apparently a complex of discrete spawning stocks.

The whitefish, chub, and herring stocks have been heavily exploited, probably to excess, as suggested by Lawrie and Rahrer (1972). Some stocks (e.g. whitefish) were directly reduced further by sea lamprey predation, and others indirectly by the diversion of fishing effort that would otherwise have gone to lake trout. Again discrete spawning stocks are thought to have been a characteristic of these populations, and unless exploitation is severely curtailed, while and if residual numbers of each stock remains extant, it is doubtful that they will be able to regain former abundance levels without the support of new rehabilitation science.

New species have appeared in Lake Superior. The impact of the sea lamprey, and its subsequent partial control has already been discussed. The arrival and dispersal of that species was reviewed by Lawrie (1970). The alewife (*Alosa pseudoharengus*) has been present in Lake Superior at least since 1953 but has not developed a large population as yet and, therefore, cannot be considered as the significant competitor with the smaller coregonids here as seems to have been the case in some of the other Great Lakes according to Smith (1968). Smelt, first recorded in Lake Superior in 1930 (MacKay 1963), increased in abundance then appeared to stabilize in the 1950s. Carp (*Cyprinus carpio*) and rainbow trout (*Salmo gairdneri*) have been established for some years locally and seem not to have had noticeable impacts upon the indigenous species. More recently the pink (*Oncorhynchus gorkuscha*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmons have been introduced, the latter two being maintained by annual hatchery-reared plantings. The pinks have persisted in small numbers by natural reproduction and recently have noticeably increased in abundance. If their numbers continue to increase, the lake herring (*Coregonus artedii*) may be faced with significant competition for food.

Among the invaders or introductions, only the sea lamprey appears to date, to have had a major impact on the fish community. Its numbers now seem to have been controlled at a level compatible with restructuring of the former fish community. Impacts by smelt and alewives are not yet understood and may not yet be fully expressed.

Lake Huron — General reviews of events and of the current status of Lake Huron and its fish community were prepared by Berst and Spangler (1972; 1973). In many respects the history of this lake is similar to that described for Lake Superior. Huron too is a deep, cold, oligotrophic lake and is relatively unproductive, though its morpheodaphic index (Ryder 1965) is higher than that of Lake Superior. Its water quality is relatively good, being to a large extent a mixture of water from lakes Michigan and Superior together with its own small watershed which is only locally modified by agricultural and industrial/municipal development. Beeton (1965; 1969) documents and compares the changes in water quality in Lake Huron with those of other Great Lakes. Significant changes in water quality are evident in bays, such as Saginaw Bay, adjacent to centers of human activity. Berst and Spangler (1972) expressed concern about the levels of contaminants such as DDT and Hg. No doubt PCBs and perhaps others ought now to be included.

A commercial fishery harvesting whitefish, lake trout, cisco, walleye, yellow perch, and suckers began in the 1800s and production rose to a maximum of 13 million pounds in Canada about 1892 and to 19 million pounds in the U.S. about 1900. From then to the mid-1930s the landings remained relatively stable, but a gradual decline began in the mid-1930s and has continued for more than 30 years. Dramatic changes occurred in the fishery and in the fish community in the period 1940–65. The lake trout and cisco populations collapsed and populations of whitefish, suckers, sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) also declined. An increase in the yield of chubs from the earlier mean of .5 million to 5.5 million pounds in 1961 did not compensate for the loss of lake trout and ciscoes. Again, as in Lake Superior, though the direct evidence is scanty, it seems that many important species suffered from excessive exploitation at one time or another.

The impact of introductions of new species on the Lake Huron fish community has probably been more severe than in Lake Superior. The sea lamprey added its predation mortality to heavy fishing mortality in the late 1930s and early 1940s and by the early 1950s lake trout were eliminated except for small residual stocks in Parry Sound and McGregor Bay. Smelt, first reported in Lake Huron in 1925, and alewives, first recorded in 1933, invaded Lake Huron, and the abundance of both has become such that there can be no doubt of the substantial extent of their impacts on the native fish community.

The specific mechanisms of those impacts will no doubt continue to be a matter for debate. Rainbow trout, brown trout, and carp have been introduced. Important sport fisheries now harvest the naturalized populations of rainbow trout which now use many streams tributary to Lake Huron for reproduction. Predation by sea lamprey as reported by Berst and Wainio (1967) and man-made barriers on streams have probably held populations at less than their potential. Brown trout occur in small naturalized populations of lesser significance according to MacCrimmon and Marshall (1968). Carp populations have supported a modest commercial fishery since the early 1900s (MacCrimmon 1968).

Kokanee salmon (*O. nerka*) were introduced to Lake Huron in 1964 as eyed eggs. Since then some 5 million eggs, fry, and fingerlings have been planted. While natural reproduction has been observed, it is not yet known whether self-sustaining populations will become established (Collins 1971). Similarly large plantings of coho yearlings and of chinook fingerlings have been made in the lake by the State of Michigan. Again some natural reproduction has been reported (Great Lakes Fishery Commission) but it is not yet known whether self-reproducing populations will develop.

In 1969, the first plantings of splake, the hybrid between brook and lake trouts, selected for early maturity and deep-swimming tendency, were made as part of the coordinated attempt to rehabilitate Lake Huron. Theoretically, because of their early maturity, it is expected that the hybrids will surpass native lake trout in their potential to develop self-sustaining populations in the presence of exploitation by the fisheries and by a residual lamprey population. Performance of the planted hybrids has provided grounds for guarded optimism that the experiment may be successful. Some natural reproduction by planted splake has occurred (G. R. Spangler, personal communication) but the capacity of the present genetic mix of splake being planted to adapt to the variety of spawning shoals formerly used by lake trout stocks remains a concern.

In summary, it appears that the quality of Lake Huron as a fish habitat is still reasonably good, except in specific local situations. The program of the International Joint Commission offers hope that it will remain so. The predatory sea lamprey population has been controlled, at least to a considerable extent. The instability of the present fish community is not yet arrested, but workers are optimistic that reestablishment of a dominant piscivore, in this case, splake, will contribute to stabilization. The extent to which the original productivity of the former fish community of Lake Huron will be regained remains an open question. The impact of smelt and alewives under stability is unknown, and the success of splake as the top predator has yet to be determined. In any event, the science presently available, together with an experimental approach, must be applied over the next decade if Lake Huron is to again achieve its potential to supply protein and recreation.

Lake Erie — In contrast to the other Great Lakes, Erie is relatively warm, shallow, and highly productive. The commercial fish harvest has remained relatively constant at approximately 9 kilograms per hectare per year over the past 150 years (Regier and Hartman 1973). The species composition of the harvest, however, has changed many times during that period, particularly since 1920 (Hartman 1972) and presently consists primarily of rainbow smelt and yellow perch. The high value species: lake trout, whitefish, lake herring, blue pike (*Stizostedion vitreum glaucum*), and walleye, each of which formed an important component of the harvest at one time, are no longer significant in the catch, and in some cases have disappeared completely. Although the average summer water temperature has increased by 1.1 C (Beeton 1961); nutrients have increased several fold (Beeton 1965, 1969; Harlow 1966); and species dominance has shifted to shorter-lived, more opportunistic species (Hartman 1972), total production has not increased as might have been expected (Colby et al. 1972). It appears that accelerated enrichment, even in lakes well suited to nutrient cycling, such as Erie, can extend to the point where the lake may be rendered less productive by oxygen deficits (Ryder et al. 1974).

Lake Erie has apparently not provided greater yields in spite of its warmer water, and greatly increased nutrients. Its yield, in terms of constant value dollars, has decreased in value through the sequence of dominant species. An introduced species, smelt, and a former junior member of the community, yellow perch, now dominate the lake and both species are fluctuating widely.

Much has been written about Lake Erie as a fish habitat, and about Lake Erie's fish. Most useful in the context of this paper are the long-term perspectives provided by Hartman (1972) and by Regier and Hartman (1973). To some degree they resolve the long-standing debate between Langlois (1946) and Van Oosten (1948) by indicating that both were partly right and that exploitation, accelerated eutrophication, and spe-

cies introductions have combined in Lake Erie to produce the present unstable situation.

Much of what was characteristic of Lake Erie has no doubt been irretrievably lost. Nevertheless an effective rehabilitation program could be expected to provide an increased total yield, an improved species composition in terms of having a dominant piscivore reestablished in the community, providing more stability, and in terms of value/pound in harvest.

The program being coordinated by the International Joint Commission on Lake Erie as on other Great Lakes will hopefully achieve a decrease in the rate of nutrient enrichment. Hopefully also the nutrient loading can be reduced to a level which Lake Erie can accommodate without loss of productive capacity from oxygen-poor areas. Contaminant reductions can also be expected. These and other water quality management measures may provide improved physical conditions on spawning grounds traditionally used by species such as walleye and blue pike (Regier et al. 1969).

The extent to which former water quality will be regained as a result of current programs has yet to be measured. Rehabilitation of Lake Erie's fish community must await the measurement before the attainable species components can be identified. If, for example, the water quality extant in the 1950 decade is again achieved, it might be possible to reestablish walleye or a mix of blue pike and walleye as dominant predators in the fish community. If, on the other hand, water quality can be improved only to the level extant in the 1960s it is doubtful that walleyes could be reestablished in dominant numbers and consideration of alternatives may become necessary. An alternative such as a walleye modified through selective breeding and/or hybridization with the European zander to achieve a stock more tolerant of highly eutrophic conditions might be appropriate. This sort of alternative seems less risky than ad hoc trials of exotic warm-water predators.

Lake Ontario — The smallest and most downstream of the Great Lakes, Lake Ontario, formerly a typical deep, cold, oligotrophic fish habitat and community, now presents the greatest challenge to the science available for rehabilitation. Though even under the best conditions its total productivity would be less than that of other Great Lakes, its proximity to major population centers greatly emphasizes the importance of its fish production.

Christie (1972; 1973) provided comprehensive chronicles of events in the fish community and habitat from the 1800s through to the present. His evaluation of the interactions between the fish community and major stresses introduced in those papers was extended in his 1974 contribution. Other, and for the most part, complementary interpretations of events and impacts may be found in Colby et al. (1972), Smith (1972), and Ryder et al. (1974).

Lake Ontario has been seriously degraded as a fish habitat in the open lake, in inshore areas, and in its watershed. Water chemistry changes in the open waters have closely followed those of Lake Erie (Beeton 1965), from which it receives most of its water. The inshore areas, vital to productivity, constitute only a narrow ribbon around the perimeter of the lake, the Bay of Quinte, and to some extent, the eastern basin excepted. The poor quality of the Bay of Quinte as a fish habitat is described by Hurley (1970; 1973) as being comparable to Lake Erie. The damage to fish habitat in the tributaries occurred during the 1800s as a consequence of land clearing which modified flow regimes and water temperatures, and as a result of construction of dams on almost all streams.

The original fish community is now in complete disarray and some of the original species components must be considered extinct in the lake. In the open lake the chief piscivores, lake trout and burbot, began to decline in the late 1920s and reached virtual extinction by 1950. Excessive exploitation and sea lamprey predation are considered to have caused the collapse of these species (Christie 1973). The deepwater ciscoes and lake herring, formerly abundant in the lake, are no longer significant components of either the harvest or of the fish community. Some species of ciscoes are apparently extinct. Heavy exploitation and interactions with invading species are thought to have been causes of the declines in these species. Lake whitefish, for many years an important species in the commercial harvest from the eastern basin, declined abruptly during the 1960s. At least one major, and likely discrete stock, which spawned in the Bay of Quinte, appears to be extinct. Another stock which spawns on the south shore of Prince Edward County persists, but at a precarious level. Alewives and rainbow smelt, both invading species, are now the most commonly encountered species in the open lake.

In the inshore zone, changes in the fish community are also evident, though they have been less thoroughly documented. In general the piscivorous pike, smallmouth bass, and walleye have undergone recent declines, the most spectacular being that of the walleye which had been so

abundant during the 1950s and early 1960s. Other noteworthy events include the invasion by which perch (Scott and Christie 1963) and their subsequent establishment at a high level of abundance in the inshore zone, and the recent extension of the yellow perch distribution to the eastern basin.

In the tributaries, rainbow trout, an introduced species, has been successful in occupying some of the degraded habitat formerly used by Atlantic salmon.

In summary, Lake Ontario and its fish community have suffered from excessive exploitation, from excessive nutrient loading, contaminant loading, shore-line restructuring, and watershed modification; and it seems to have had more than a fair share of new species invasions.

The program of the International Joint Commission holds promise of improved water quality. Indeed "Project Quinte," a current multiagency effort, may measure the first response of habitat and fish community to such a program in the Great Lakes. Sea lamprey predation is being controlled by the Great Lakes Fishery Commission. Planting programs involving lake trout, splake, coho, and chinook have demonstrated that the lake can still provide good growth and survival of premium fish species. The challenges for rehabilitation include: achieving balanced and controlled exploitation levels, reestablishing natural reproduction by salmonids and coregonids, and possibly reestablishing species such as the deepwater sculpin which may be a necessary link in nutrient vectoring. Current studies of shoals formerly used by lake trout for reproduction, together with progress in water quality management, may provide a basis for considering spawning ground rehabilitation projects.

Some other examples — There is a frustrating scarcity of good time series data for small freshwater lakes and streams. Only four "small" oligotrophic lakes in Canada Keller (Johnson 1972), Great Slave (Keleher 1972), Kootenay (Northcote 1972), and Opeongo (Martin and Fry 1972), with adequate data series were offered as contributions to the objectives of SCOL symposium (Loftus and Regier 1972). There is little doubt now, however, that several additional "case histories" could be found and that useful data series for mesotrophic and eutrophic waters exist. Considerable data, however fragmentary, are available from a great many fresh waters and some are used here against the background of the inferences from the SCOL symposium. In doing so, on a broad scale, it is difficult to avoid pessimism concerning the status of freshwater fish communities in general such as was evident in Ryder and Johnson (1972) when they considered the future of North American oligotrophic lakes.

Lake Simcoe contains a salmonid community which has provided up to one million angler days per year to the people of nearby metropolitan Toronto. This resource, which has immense value, appears to be under severe stress. Oxygen deficits are beginning to appear in some bays. Phytoplankton and benthos species changes are occurring, and the distribution of aquatic plants is shifting. The age structure and abundance of the lake whitefish population is changing and there is a strong suggestion of recruitment failure. Lake trout angling is supported to an increasing extent by hatchery plantings. Rainbow smelt, introduced in the late 1950s or early 1960s have achieved a considerable level of abundance and now appear to have stabilized. Lack of stability is becoming evident in the smallmouth bass population, and yellow perch are currently greatly expanding both range and abundance.

Relatively good data suggest that there has not been excessive exploitation. The current responses in the fish community and the habitat implicate impacts by the newly established smelt and more particularly by cultural eutrophication. Municipal and cottage development have been extensive and the nutrient loading may have been excessive. Heavy fertilizer use in an area of intensive agriculture adjacent to part of the lake no doubt contributes further nutrients.

Some reduction in nutrient input is likely in the near future when appropriate municipal sewage treatment facilities are completed. Early application of a multifaceted rehabilitation program might prevent the collapse of the trout and whitefish stocks and might restabilize the fish community.

The Muskoka lakes are intensively used for water-oriented recreation and have been extensively developed for cottagers. Nutrient loading of the lakes from the cottages, an extensive DDT spraying program aimed at control of biting flies, and invasion by rainbow smelt all have been suggested as contributors to stress on the fish communities of these lakes. Lake trout no longer reproduce naturally except to a limited extent in Lake Joseph. Attempts to provide lake trout angling by the traditional yearling plantings failed, but some success has been achieved using 2-year-old fish. Are there alternatives to this expensive technique of providing recreational angling?

Lake trout populations, and salmonid communities throughout Ontario and perhaps throughout Canada are under considerable stress occa-

sioned by man's activities. Almost all our lakes are now accessible during summer and winter, with the advent of more leisure time, dollars, roads, and the snowmobile. There have been reports concerning small lakes where more than a year's production of lake trout has been taken by anglers on a single weekend (Ryder and Johnson 1972). The popular myth that decreasing angling quality acts to curtail exploitation short of overexploitation must now join the formerly popular and similar myth about exploitation by commercial fisheries. Rehabilitation of the trout stocks requires much more stringent controls on exploitation. The challenge lies in achieving the kind of public involvement and commitment which is essential in support of more complex and restrictive regulations, and in maintaining client expectations at levels consistent with the natural productivity of waters. Although we have yet to achieve a rational basis for allocating limited resources between commercial and recreational users, the new tasks of allocation between resident and nonresident anglers, and of allocation among resident anglers are upon us.

Mesotrophic and eutrophic lakes and their respective fish communities no doubt have greater capacity to accommodate stresses than do oligotrophic lakes and their salmonid communities (Ryder et al. 1974). For lack of alternatives, the inferences which emerged from SCOL for oligotrophic lakes and their fish communities are here applied to other lake sets and fish community types. The absolute stress levels triggering response in these categories of lakes are no doubt substantially different.

There are scattered data to indicate that changes are occurring in the fish communities of some of the Kawartha lakes, the Rideaus, Nipissing, Eagle, and other nonsalmonid communities. One might view these with less concern were it not for the knowledge of past events in some bays in the Great Lakes which may well be to a large extent comparable to small mesotrophic or eutrophic lakes. Examples include the Bay of Quinte, Lake Ontario (Christie 1972, 1973, 1974; Hurley 1973), Green Bay, Lake Michigan (Wells and McLain 1972), Saginaw Bay, Lake Huron (Berst and Spangler 1972), and the western basin of Lake Erie (Hartman 1972; Regier et al. 1969). In these cases the fish communities were dominated by walleye during what appeared to be a relatively stable time, environmentally. Subsequently, however, the walleye has lost its dominant position and has all but disappeared in some cases. Lack of stability and decreased resource value has been characteristic of the resulting species communities which have developed since. It seems likely that present indications from some percid communities in smaller inland lakes foretell a similar sequence of events. Exploitation can be intense as shown by Jorgensen (1975) for Lake Nipissing where the estimated poundage of walleye taken by anglers in a year is equal to the potential total yield (calculated as per Ryder 1965). Nutrient loading from natural sources, augmented by that from intensive cottage development (Dillon and Rigler 1975) and from the recently recognized atmospheric source may be such as to severely stress even these lakes.

The problem of nutrient loading, and the stress components associated with cottage development, is emerging as a major concern in Ontario and at least locally, throughout the lakes and streams of Canada. Oligotrophic lakes, those with the least capacity to accommodate stress, are the most attractive for development probably because of their size and their aesthetic appeal. Most lakes south of the French and Mattawa rivers in Ontario may already have been developed for cottaging up to or beyond their capacity. This appears to be the case also for a surprising number of lakes in northern Ontario. The pressure for continued development is severe and fisheries managers are hard pressed to resist the well-established trends. There is an urgent need for a clearer and a quantifiable understanding of the capacity of type lakes to accommodate the stresses associated with cottage development. A simple, predictive index to nutrient loading and to capacity is urgently required and may well emerge from research directed at meshing Ryder's MEI and Dillon and Rigler's (1975) nutrient loading models. Meanwhile, the challenge to the science of rehabilitation may lie in the development of techniques to reduce nutrient loading in overdeveloped lakes, until such time as the nutrients are otherwise excluded.

Anadromous stocks of fish in Ontario have received relatively little attention, perhaps because of the overpowering nature of other larger problems. Nevertheless, the production from rivers and streams is important and the discrete stocks of brook trout, rainbow trout, walleye, and formerly lake trout, using streams tributary to the Great Lakes for spawning, have been actively exploited. Pollution from point sources and artificial flow regulation have contributed to the decline and/or loss of some stocks (Ryder 1968; Winterton 1975). In the case of rainbow trout, particularly in the lower Great Lakes, considerable suitable stream habitat has been lost due to the extensive construction of small dams, many of which no longer serve the purposes for

which they were constructed. There is considerable interest in the development of strains of rainbows which would be less demanding of quality stream habitat, perhaps spending only one year rather than two or three in the streams.

Stream habitat management has been shown by Saunders and Smith (1962a and b) and by White and Brynildson (1967) to enhance trout production. No serious attempt to apply this homespun science has been made in Ontario or in any of the freshwater areas. Perhaps these techniques are too unspectacular for popular use, or perhaps their application is looked upon as the fine-tuning management which comes after the big problems are solved. In any event application of this science now, as part of a rehabilitation initiative, seems necessary at least at the level of demonstration projects, and as a means of gaining some necessary experience.

Small lakes and ponds collectively play an important role in fish production across Canada, and considerable science for their management has been developed. In Ontario, for example, much of the brook trout production is provided by these small lakes and ponds. Many have limited or no capacity to sustain natural reproduction and their continued productivity is dependent upon routine hatchery plantings (Fraser 1972). J. M. Fraser (personal communication) also reported that the presence of any other species, particularly suckers and yellow perch, detract greatly from the capacity of such waters to produce trout. Recently there has developed evidence (J. M. Fraser, personal communication) that plantings derived from long-domesticated, hatchery brood stocks are subject to higher mortality rates after planting than are plantings derived from wild brood stocks.

The recent work with rainbow trout in prairie "pothole" lakes (Lawler et al. 1974), has attracted considerable attention. Initial results indicate a considerable yield, but long term sustainable yield has yet to be established. Further progress in this promising area apparently requires the ability to select better "strains" of rainbows for stocking, and the further development of more sophisticated criteria for the selection of most suitable "pothole" lakes.

Although most examples discussed in this section have been Ontario waters, reflecting a personal experience bias of the author, there is ample evidence that similar problems requiring rehabilitation initiatives are becoming commonplace in other areas of heavy use across Canada. In British Columbia a number of trout lakes are being recognized as problem areas: Kootenay Lake as reported by Northcote (1972), and Paul Lake, where cottage development has been extensive, are cases in point. In the Prairie Provinces there are examples of problems rising out of exploitation and eutrophication in waters such as the Qu'Appelle lakes, Great Slave, Lesser Slave, Athabaska lakes, and Lac la Ronge. In most of these some stocks of lake trout and perhaps other species require rehabilitation if former production levels are to be regained. It has been generally understood that the waters of the north and their fish communities have relatively little capacity to accommodate stress, whether exploitation or eutrophication, but the resolution of that understanding needs to be improved considerably and urgently. Although I am not aware of specific problem waters in Quebec or the Maritime Provinces, there seems no doubt that rehabilitation needs are generally comparable to those identified in the foregoing example.

A Summary of Stories

All fisheries discussed in the foregoing sections are now far less productive in terms of high value protein and/or quality recreational opportunities than formerly. The Perspectives by Regier and McCracken (1975) and by McCracken and Macdonald (1976) indicate that this condition is more typical than exceptional in most important fisheries of Canada. Only the scattered, but locally very important, fisheries of more northern inland Canada can still be managed using a conservation or maintenance approach (Regier 1976). Almost all our major fisheries require rehabilitation.

On the west coast it has been estimated that current levels of salmon yield are about half of the levels produced in earlier years. It is recognized that some of the historical harvest figures were in excess of the levels that one might expect to maintain in the long term, nevertheless, a rehabilitation initiative designed to achieve full access for a natural, wide variety of stocks to improved freshwater environments could provide for a doubling of the present allowable harvest, if that harvest could be tuned to a stock-by-stock basis.

On the east coast it appears that the brook trout resource is relatively healthy, but could be improved to a valuable extent if stream engineering sciences were applied. The Atlantic salmon, on the other hand, is a severely depressed resource which will require major initiatives if it is to be restored to former abundance levels, estimated at two to four times the present level.

In the freshwater area, represented by the intensively used Great Lakes, the present fish re-

source situation is, in a sense, depressing because it clearly demonstrates the impact of overexploitation of the fish stocks in combination with the stresses imposed by conflicting use of the habitat. The result has been a serious reduction in total yield and a major reduction in quality yield. This area provides a case history of immeasurable predictive value to the rest of Ontario and Canada. In another sense the extremity of the responses in these fish communities have contributed to the surfacing of a public concern which now supports international agreements and programs for agencies such as the Great Lakes Fishery Commission and the International Joint Commission and these constitute the first essential steps to the rehabilitation of traditional fish yield capacity.

Overexploitation emerges as a major problem for fisheries managers in all areas discussed. The evidence implicating overexploitation as a significant stress has always been imprecise because of the masking effect of other stresses, and has always been clearly evident only after the fact of depressed or collapsed stocks. Furthermore, the evidence has been available only on a piecemeal basis through time. Hindsight is much more convincing than foresight but even the former has proven inadequate to achieve effective control in the face of the associated social and economic problems. We are still faced with inadequate control of fishing power, real or potential, in most areas.

Cultural eutrophication, the addition of excessive nutrients, shoreline modification, and chemical pollutants have recently been recognized as an important complex of factors having impact on the productive capacity of natural waters. The impact of chemical pollutants on the east coast has been particularly well documented. In the freshwater area the effects of DDT, mercury, and PCBs are now obvious and the inference that new chemicals will be identified as deleterious is ominous. The significance of air-borne sources of chemical inputs which will be quantified shortly, is expected to be significant.

Extensive cottage and recreational development on the shores of freshwater lakes has become a matter of serious concern for fisheries managers. This concern is not unimportant in terms of demands on the fish communities, but the major concern is the apparent cultural eutrophication imposed on the lakes with resultant loss of both yield and aesthetic values.

On both sea coasts the fact of pollutant concentrations in estuarine areas is emerging.

In all three areas discussed, man's activities on the watershed have resulted in barriers to the migration of anadromous stocks, and have degraded the productive capacity of the streams by virtue of sedimentation and by modifying natural flow regimes. The most spectacular examples of barriers to migration are evident on the coasts, and the most extreme cases of stream degradation are found in the watersheds of the lower Great Lakes.

The impact of species introductions and/or invasions is particularly evident in the freshwater area. This evidence may have relevance to current marine situations yet to be recognized.

While considering the sequence of historical events in the foregoing fisheries as background for their rehabilitation, it has become evident that the significance of discrete stocks may be far more important than has been explicitly realized to date. Attention, thought to be appropriate, is focused in the section which follows.

The Stock Concept

The reality of discrete spawning populations has been recognized for several years as an important consideration in the management of west coast salmon. There has been an explicit attempt to harvest each recognized stock at the different levels appropriate to their continued productivity. In practice, however, this laudable and necessary objective has been difficult to achieve with more than general precision because of the mixing of stocks at sea, and because most of the harvesting gear does not discriminate between stocks. Only when the stocks are close inshore and near their "home" stream do they become adequately separated to allow an opportunity for fully selective harvesting. By the time this sort of separation occurs there is little, if any, opportunity for harvest by the traditional gear, and furthermore, the quality of the fish may have seriously deteriorated.

In spite of the difficulties, the objective has been partially achieved and, in the process, much additional information on the movements and distribution of stocks in the ocean has been generated.

Ricker (1972) presented a comprehensive review of the knowledge of discrete stocks of west coast salmon and trout. Impressive indeed is the listing and description of discrete stocks within species, and particularly within single river systems. The question whether genetic and/or environmental influences are involved in the emergence of discrete stocks is vital to management and to rehabilitation. The epilogue of Ricker's exhaustive work is, therefore, quoted here.

> "In almost all cases where both genetic and environmental influences affecting natural

stock differences among Pacific salmon and steelheads have been searched for adequately, both have been found; though sometimes one, sometimes the other, is relatively weak, or is infrequently expressed.

"Since season of return to the river is strongly under genetic control, and ability to 'home' is apparently under genetic control, a corollary is that most or all of the identified stocks of these fish differ genetically to some extent.

"Such conclusions sometimes encounter criticism on the grounds that they are too complicated. Nature (the argument runs) should not be made more complex than it really is; species can exist in one and the same river system, a dozen or so even within a single lake — particularly when it is known that there is some interchange between them.

"Certainly when two or more hypotheses are equally possible, it is customary to prefer the simplest one. But how are we to know which one is simplest? What is the test of simplicity? With respect to any recurring difference between two salmon stocks, we have three alternatives:

"1. The difference is completely environmentally determined.

"2. The difference is completely hereditarily determined.

"3. The difference is determined partly by heredity, partly by environment.

"Superficially at least, hypothesis (1) and hypothesis (2) both seem simpler than hypothesis (3); perhaps they really are so.

"If we were to reject hypothesis (3) because it is too complicated, then which of (1) and (2) is the simpler? Some writers have seemed to believe that (1) is simpler than (2), or at least 'more conservative' than (2), apparently because it implies a more homogeneous genetic constitution among the various populations of a species. For example, if it has been demonstrated that the number of scales on fish of a certain species is affected by environmental temperature during development, they will then decide that 'there is no need to postulate' any genetic basis for an observed difference in scale number between two local stocks of that species.

"But what if we were to apply the same procedure in reverse? Suppose we have demonstrated a hereditarily-determined difference in scale count between two stocks, as Dr. Neave did for *Salmo gairdneri*; should we then decide that there is no need to postulate any effect of the environment on scale number in that species? That obviously isn't logical; but then the converse proposition cannot be logical either.

"My strong opinion is that we should avoid any appeal to simplicity or conservatism in such questions. Time and again it has been discovered that nature is more complex than anyone dreamed possible. Hence we should stick to whatever evidence is available, however sketchy it may be.

"In the matter at hand, the evidence available is now quite considerable. It indicates that most of the studied differences between local stocks can and usually do have both a genetic and an environmental basis. Be it simple or complex, this should now be our normal expectation in respect to any as-yet-unstudied difference between stocks of salmon or trout. Only direct investigation can show which type of influence predominates in a particular situation."

Larkin (1972) provides a view of the management implications of the stock concept. The difficulties in achieving selective harvest of discrete stocks are emphasized.

Available evidence strongly suggests that full utilization of complex river systems by salmon, giving maximum production of young salmon from the system, and maximum returns to it, is achieved only when a complex of stocks is present. Salmon rehabilitation projects face the task of optimizing reproduction on a stock-by-stock basis and of learning how to recognize or to create stocks comparable to those which have already been lost. Care may be necessary to avoid overloading parts of the river system to the detriment of other stocks and projects will require careful balance between stocks and careful evaluation.

The significance of discrete spawning stocks is recognized now as well in Atlantic salmon (Saunders 1967; Moller 1970; A. W. H. Needler, personal communication). Probably because of the relatively small size of the total resource and because it is comprised of small runs scattered over so much coastline, less detail is available to describe these stocks. Less is known too of the movements of separate stocks at sea, witness the recent surprise off Greenland which precipitated harvest restrictions. It seems probable that many stocks have already been lost and that rehabilitation will be the more difficult for that reason.

In the freshwater area little attention has been given to the significance of discrete spawning stocks. I am now of the opinion that our inattention in this respect may have rendered some of our management ineffective, and in some cases where routine plantings have been involved, even counterproductive. A few examples may serve to establish the possibility of parallels in some freshwater species to the stock concept described for Pacific salmon.

Martin (1957; 1960) described very precise homing behavior in lake trout at spawning time

in 1480-acre Louisa Lake where the spawning grounds were separated by only a few yards. His confirming evidence of discrete spawning times and within-lake locations for lake trout in a number of Algonquin Park lakes (personal communication) is extensive. Loftus (1958) described populations of river-spawning lake trout in Lake Superior. The distribution of these trout stocks overlapped in the open lake but they separated year after year and moved to the "home" (presumably natal) rivers. He recorded some additional spawning times and places for Lake Superior lake trout as reported by fishermen and hatchery personnel. Eschmeyer (1955) in discussing lake trout reproduction in southern Lake Superior suggested that lake trout returned to the same spawning shoals year after year. J. B. Smith (1968) was able to map more than 150 separate former lake trout spawning grounds on the basis of recollections by commercial fishermen. Lawrie and Rahrer (1972) and Regier and Loftus (1972) considered that the system of accumulating catch statistics in Lake Superior and in other lakes, a system which did not reflect stock-by-stock distribution, served to mask the reality of the fishing-up process to the extent that some stocks may have been decimated long before total harvest figures showed a decline. In many instances, the trout rehabilitation program in the Great Lakes implicitly, but not explicitly, recognizes the stock concept. Successful rehabilitation may be delayed by the lack of appropriate brood stocks. Olver and Lewis (1971) were able to find only a few examples of planted lake trout which successfully reproduce themselves.

Whitefish in Lake Huron are comprised of apparently discrete stocks. Two are recognized by J. J. Collins (personal communication) in the North Channel; two in South Bay (Budd 1957); two in Georgian Bay (Cucin and Regier 1965), and two in Lake Huron proper (Budd and Cucin 1962; Spangler 1974). These stocks may be the few remaining from a larger original number of stocks. Christie (1972) recognized two stocks of whitefish in Lake Ontario, one of which now appears to be extinct.

Walleye literature also suggests strong parallels to the stock concept. Lake Erie contains two apparently discrete stocks, one which reproduced in the Western Basin and which has suffered a severe decline in recent years; another which reproduces in the eastern basin and which has remained relatively stable. Ferguson and Derksen (1971) described mixing of a Lake St. Clair walleye population with those of southern Lake Huron and of western Lake Erie. In the Bay of Quinte, Lake Ontario, Payne (1963) studied a population, then flourishing, now virtually extinct. Within the same bay certain river spawning populations persist at low levels (W. J. Christie, personal communication). In Lake Huron a number of discrete river spawning walleye stocks are recognized in the Moon, Shawanaga, French, Pickerel, Mississauga, and Echo rivers. Others no doubt occur. The same story is probably verifiable for stocks in Lake Superior's Goulais, Batchawana, and Michipicoten rivers, and Ryder (1968) recorded the demise of one such population near Red Rock in Nipigon Bay. The work of Uthe and Ryder (1970) presents further evidence that the stock concept may be valid for walleyes.

Rainbow trout, a species introduced to the Great Lakes several decades ago have now become naturalized and appear to exhibit "stock" characteristics similar to those described for steelhead on the west coast.

To date the significance of discrete spawning stocks, the stock concept of west coast salmon, appears to have failed to attract the explicit attention it merits for management and rehabilitation throughout the freshwater area.

It is recognized that many stocks are seriously depressed and that some have already been lost. There are a number of causes for these losses which need to be more widely recognized, better understood, and guarded against. They include (1) direct excessive exploitation, (2) incidental catch by gear directed at adjacent stocks or species which are in good supply, (3) genetic drift imposed by the selectivity of gear fishing for a particular size. This may tend to remove early maturing and/or fast growing individuals from the stock, (4) hatchery plantings from unselected stock origins may survive to maturity and mix with native stock during spawning thereby diluting the gene pool of a well-adapted stock, (5) environmental change may force desegregation at spawning of formerly discrete but closely related stocks causing interbreeding. No doubt a number of other mechanisms could contribute to loss of stocks essential to the full use of an ecosystem.

Over several thousands of generations, most species appear to have evolved discrete stocks adapted to similar yet discrete and specific habitats. Fisheries science is not yet able to recognize either the habitat differences or the specific characteristics which differentiate stocks. Man's attempts to date to move stocks from one place to another have been mostly unsuccessful at least in terms of achieving natural reproduction by the transplanted stock. Given that a naturally evolved complex of stocks is apparently essential to full

use of the productive capacity of a river system, and perhaps of lakes, it follows that it is important to learn to recognize and to preserve representative stocks. It is also important to learn how to reestablish stocks which have been decimated or lost, and to achieve a natural balance among stocks. There is a strong implication that rehabilitation requires the culture and planting of numerous small lots of the appropriate stocks until natural reproduction is reestablished. Such planting requirements suggest a need for small, versatile, and mobile hatchery facilities rather than the major "efficient" fish factory type of facility currently in favor.

It may be necessary to establish a national gene pool which would provide for the preservation of representative, particularly valued or endangered stocks.

Rehabilitation vs. Sea Ranching (Fish-Farming)

Emphasis in the foregoing section has been given to the stock concept and to the conclusion that a naturally evolved complex of stocks is required to fully use, and perhaps to provide relative stability in, an ecosystem. The maintenance or rehabilitation of such stock complexes is judged to be the most suitable goal for fisheries ecologists and managers for a number of reasons, and ought to provide the best returns over the long run. Attainment of this goal is likely to be a slow, deliberate, and unspectacular process requiring careful research and management involving both the fish and their habitat.

The term "enhancement" has been in vogue among fisheries people recently. Use of the term is deliberately avoided throughout this perspective because it apparently has a variety of meanings. To some it carries the implication that the approach to increasing the abundance of fish to earlier levels ought to be as described above. To others it appears to imply a massive fish culture program which assumes that catches are roughly proportional to the numbers of fish planted. Still other fisheries people think in terms of some undefined mix of the two approaches.

There is ample recent evidence that massive planting programs can produce spectacular results, at least in the short term. Particularly impressive examples have been recorded with salmon in the Pacific northwest states, and with salmon in Lake Michigan. Such successes as these may have created the environment in which fisheries "enhancement" projects can be optimistically put forward. It needs to be recognized, however, that both these successes occurred in situations to which fisheries people do not normally aspire: in the northwest U.S. the freshwater productive capacity has been lost to a very major extent; in Lake Michigan the original fish community was in disarray and had included no dominant piscivore for three decades.

The recent successes ought not obscure the longer-term experience of lack of spectacular success from fish planting. No doubt there have been improvements in fish culture techniques which have contributed to recent successes, but the important difference between earlier and recent fish planting results seems more likely to be the "health" of the community into which the fish are planted, as suggested by Christie et al. (1972).

It is difficult to argue against the recently demonstrated successes of sea ranching or fish-farming (e.g. Lake Michigan, Washington State), and such an argument is not intended. Such an approach to fisheries management may be the only option available where the natural system has been degraded beyond hope of recovery. This is not our situation in Canada, even in the Great Lakes, except perhaps very locally. There are abundant grounds for optimism that our aquatic habitats will be maintained, and where necessary improved.

If we were to take the sea ranching option at this time we could expect:

1) spectacular successes (in terms of returns from planted stocks, but not in terms of natural reproduction), at least in the short term in carefully selected locations, e.g. lower Great Lakes, Georgia Strait;
2) creation of client appetite;
3) raising client expectations (they are already excessive from past overexploitation experience);
4) demand for program expansion to other areas where success would be less likely;
5) reduced success levels, occasional stocking failures;
6) loss of opportunity to rehabilitate fish stocks in healthy areas (demand would force managers to the sea ranching option);
7) loss of important natural stocks (by virtue of incidental catches or by swamping them competitively in the short term);
8) loss of our solid base from which to argue for aquatic environmental quality.

Sea ranching, or fish-farming may well be an appropriate initiative in Canada at the present time. It could pay substantial returns in specific situations. Furthermore, its demands of science

are generally similar to those required by rehabilitation. Its undertaking, however, requires a clear-cut policy decision which would include the dedication of prescribed aquatic habitat for the purpose, and a clear recognition of the spill-over effect on other management initiatives. Sea ranching ought to be seen as having implications which conflict with rehabilitation. The term "enhancement" which confuses this important distinction ought to be dropped.

Science Needs for Fisheries Rehabilitation

In anticipation of major initiatives in rehabilitation on the west coast, fisheries managers and researchers have given considerable thought, both separately and jointly, to the kinds of work that needs to be done to assure maximum benefits. In the freshwater area, a joint Federal–Ontario strategic plan for fisheries is nearing completion. That joint planning effort was undertaken primarily as a result of recognition that past fisheries management practices have proven inadequate, and secondarily, as a result of the recent major advances in our understanding of man's impact on fisheries as crystalized by the SCOL symposium. On the east coast similar planning efforts by Fisheries and Marine Service staff are in progress. It is not intended in this perspective to attempt to second guess the excellent and detailed strategies that have emerged from any of these planning efforts, rather it is hoped to provide some general focal points for science as it seems appropriate to fisheries rehabilitation initiatives throughout Canada.

Fish Stock Manipulations

Exploitation control — There is need for a substantial improvement in the capability to selectively harvest discrete stocks, to avoid or precisely measure incidental catches, and to finely tune total harvest on a stock-by-stock basis to predicted allowable harvest levels. The science needs implied in the foregoing include: studies designed to refine gear selectivity; studies of stock distribution and movements; and studies designed to provide more reliable allowable harvest prediction. Perhaps even more important, however, is the implied need for rationalization, at the policy level, of the total fishery, and of the allocation between client groups; development of a strong "partnership" atmosphere between client groups and managers; and perhaps new institutional arrangements for management decision making and delivery.

Hatching, rearing, and planting — Many rehabilitation projects will require products from fish culture facilities until naturally reproducing stocks can be reestablished at appropriate levels. Most of the science basic to the hatching, rearing, and planting of salmon and trout is now available. The application of this science, however, is far from uniform throughout Canada, even within regions. Many research and management projects have failed, and will fail, because the health of fish from the hatchery has been taken for granted. Little recognition of the significance of the "stock concept" has been evident until very recently. A more adequate and uniform application of science probably requires modernization of many of the existing fish culture facilities, and an explicit recognition of fish culture as a profession requiring for its successful practice, a high level of specialized training.

Fisheries rehabilitation in the next several decades will require both transfer and extension of available science. The science available for salmon and trout will have to be effectively transferred to professionals, yet to be appointed in many areas, in the fish culture system. The science of walleye culture which has emerged from work in Oneida Lake, New York, and in Iowa, Wisconsin, and Minnesota needs to be assimilated for use in Canada. Similarly the coregonid culture experience of European colleagues needs to be transferred to Canada. The science available for both walleyes and coregonids will undoubtedly require extension and refinement for our rehabilitation programs. Furthermore, in efforts to rehabilitate fish communities which have collapsed as in Lake Ontario, it may be found necessary to learn to culture essential nutrient vectoring species such as the deepwater sculpin, now virtually extinct.

In the most recent thinking on the west coast it seems generally accepted that rehabilitation cannot safely be targeted on a single species, or a single stock within a river system without placing adjacent species and stocks in jeopardy. Here and elsewhere it is becoming apparent that species and stocks must be rebuilt in a balanced community. Recognition and implementation of the foregoing considerations may require extensive modification of the traditional fish culture station design, and will certainly extend the demands upon fish culturists for scientific performance.

Fish health — The current situation appears to be one where many, if not all, fish culture facilities have problems with fish diseases and para-

sites. The extent of these problems is difficult to describe in specific qualitative or quantitative terms because of generally inadequate diagnostic services and because agencies have only recently appreciated the need for accurate records in this respect. In any event, mortalities among fish in culture frequently result in substantial investment losses which ought to be measured and if possible avoided. Furthermore, it is not uncommon to learn that fish in questionable health are planted as part of routine programs, or are made available for research projects. The financial losses and/or ecological consequences of such action must be a matter for speculation only. The foregoing statements are personal, and are not made with any derogatory intent at all. They are intended only to *identify* a problem of serious proportions so that it can be faced and solved by the application of appropriate diagnostic and prophylactic services.

Aggressive fisheries rehabilitation programs will require additional fish-rearing capacity, and perhaps more importantly, will shift the emphasis to a broader spectrum of species and of discrete stocks in culture. Some stocks will be the more valuable because of their rarity, others because they will represent considerable investments of time, money, and science in their selection and breeding.

Important planning initiatives have recently been taken in the area of fish disease control. The Fisheries and Marine Service of Environment Canada have developed, with participation by provincial and university representatives, a draft "Fish Health Protection Regulations" 1975. The Great Lakes Fishery Commission recently endorsed as policy the report prepared by its Fish Disease Control Committee (1975), a significant international development. These reports support the view that disease prevention is well worth the priority attention it now receives in new or in reconstructed culture facilities, and they underline the need for the extension of adequate diagnostic services and prophylactic practices in all fish culture facilities, including those operating in the private sector. The reports also urge the development of policies designed to inhibit the careless transfer of fish from place to place, even within regions.

Economic and ecological considerations generally, and the policy planning results in particular, imply the need for a major center, or centers of excellence for fish health work in Canada. A center should provide for both research and for diagnostic services in support of government and private fish culture and aquaculture facilities. A center should be staffed by federal, provincial, and university people and also contribute to the training of experts who will be needed in the future.

Nutrition — Many general points to which reference was made in the preceding section can be justified, in parallel, for fish nutrition. Thus, fish from our fish culture stations used in experiments and in management programs are not known to have been entirely healthy from a nutritional point of view. Furthermore, there is an often expressed opinion that some fish culture problems which are expressed as disease problems, may arise from stresses to which inadequate diets are important contributors.

Most fish culture facilities in Canada now use diets formulated outside Canada, in some cases, for species other than those being cultured here. The cost of importing preformulated food is rapidly becoming prohibitive. Formulation of similar or alternative diets, using Canadian ingredients requires nutritional expertise not readily available in Canada.

The broader spectrum of species and of stocks to be cultured during rehabilitation programs will undoubtedly require a wider variety of diet formulations than is now available. Furthermore, it is now recognized (Slinger, personal communication) that diets may require fine tuning at different fish culture stations depending on local water chemistry. A further problem emerging in fish culture is that of facility effluent quality, and again it is possible (Slinger, personal communication) that manipulation of diet ingredients may be part of the answer to this problem.

In most of the specialties of animal husbandry: chickens, turkeys, hogs, or cattle, it has been necessary to develop special diets in support of intensive culture. The anticipated level of operations in government fish culture stations, with the parallel needs of private hatcheries, and a developing aquaculture industry should constitute a market area broad enough to justify the Canadian development of special diets, particularly when locally produced ingredients can be used. A recent initiative by Ontario with experts at the University of Guelph has now been augmented by funds from the Fisheries and Marine Service in an attempt to address some of the above problems, and to spark an interest in fish nutrition.

In aquaculture the objective will be to grow, as rapidly as possible, in as little space as possible, and at least expense, fish which will be

palatable and attractive in a package. In rehabilitation programs the objective will require healthy and vigorous fish of several kinds, able to survive in natural waters. The diet requirements will be different.

A center or centers of excellence for fish nutrition, similar to the suggestion for fish health is recommended.

Fish genetics and selective breeding — A number of fish stocks on the west coast, east coast, and in the freshwater area are depressed to critical levels or are extinct. In the Great Lakes where multiple stresses have been evident, the discrete stocks lost may number in the dozens and involve species such as lake trout, whitefish and other coregonids, and walleye. In all areas, it seems prudent to accept as fact the real possibility that we have lost many more stocks than can readily be identified now. Most of these stocks have been lost as a result of man's intervention, direct and/or indirect: fishing, industrializing, dam and/or canal building, trying to reduce the nuisance from black flies, mosquitoes, or budworms, etc. We would be naive to assume that, having recognized the importance of discrete stocks, we will now be able to organize the activities of competitive water users in such a way as to avoid the loss of additional stocks.

Former high abundance levels were supported by communities of species, and by within-species stock complexes. Rehabilitation programs, therefore, are directed toward the rebuilding of these species and stock complexes to levels at which they are again able to reproduce effectively. It is intended that management will be such as to allow them to maintain themselves through natural reproduction. The implication here is that rehabilitation of the Fraser or Saint John River ecosystem, and of lakes Superior or Ontario requires the reestablishment of naturally spawning populations of each of the species and stocks which formerly made up the resource base in those waters. It is recognized that habitat degradation by virtue of new species invasions, and by water quality changes may have eliminated some of the precise habitats formerly occupied by some species or stocks, and that, therefore, we may be unable to fully regain the former levels of abundance. Aggressive habitat management programs such as those undertaken by the Great Lakes Fishery Commission and the International Joint Commission in the Great Lakes are needed to make some of those habitats available again, while others must be considered lost. Having accepted that we are unlikely to fully regain former abundance levels in our rehabilitation programs, there are still major improvements attainable.

In many instances where stocks persist, though at precariously low levels and where their habitats remain healthy, the science necessary for their rehabilitation appears to be available. In cases where stocks are at extremely low levels, it may be advisable, or necessary, to use sex products from males only for cloning with females of a closely related stock, as suggested by Calaprice (1969) and by Ihssen (1976) to obtain adequate numbers of fish containing at least some of the genes necessary to effective rehabilitation. Further careful testing of this technique would be useful.

In many cases where stocks have become extinct, and where they may go to extinction despite our best efforts, and/or in those cases where the habitats have been modified in some irreversible way, the science required for rehabilitation is not yet available. A major new initiative of basic research in fish genetics and selective breeding is necessary.

The necessary new research initiative may not be difficult to mount because scattered existing initiatives have already shown promise of success. In Ontario, for example, beginning in the late 1950s under the guidance of F. E. J. Fry, an attempt has been made to create a new trout stock by hybridization and selective breeding, capable of occupying the vacant lake trout niche in Lake Huron. Hybrids were made between lake trout and brook trout, and the selection techniques to concentrate the deep-swimming lake trout character and the early maturing character of brook trout (Tait 1970; Straight 1969) were developed and applied through four or five generations. The project has been successful in the laboratory and large-scale field testing of the selected hybrid is currently under way in Lake Huron. In this research an attempt was made to build a new trout to occupy the former lake trout habitat which has been modified by the sea lamprey invasion and the several fish community consequences of that event. It is suggested that similar research projects may be necessary for other trout, salmon, whitefish, and walleye populations where original stocks have vanished and where water management cannot be expected to restore habitats of the quality required by the original stocks.

More recently, work in selective breeding and hybridization has been initiated with salmon at St. Andrews on the east coast, Nanaimo on the west coast, and with rainbow trout at Winnipeg. Some of these studies reflect the anticipated need for selection of special characters in aquaculture programs rather than rehabilitation programs.

Whatever the specific objectives of the several beginnings that have been made, all have been contributing to a better definition of the basic questions that must be addressed by research. Some of these follow:

1. What are the mechanisms or patterns of inheritance for discrete characteristics? It will be necessary to select for certain characters (e.g. deep-swimming ability, or tolerance for low oxygen levels) and at the same time avoid the incidental selection of an unwanted character (e.g. stream spawning).
2. What are the specific parameters in a changed environment which have become critical to survival of a stock?
3. Having identified the parameters in (2), what are the selection techniques appropriate to adapting the new stock to the changed environment?
4. How are closely related stocks recognized? By time of spawning, spawning behavior, direction of fry movement after emergence, etc? It was mentioned earlier that some stocks are thought to have been depressed through genetic dilution from indiscriminant plantings of other stocks of the same species. Still the prospect of being able to select from elsewhere a stock appropriate to the vacated niche of an extinct stock is intriguing. Further, if sex products from "closely-related" stocks can be helpful in rehabilitating a critically low, or lost stock, how can the appropriate stock be identified?
5. Is the approach suggested by Calaprice (1969) and by Ihssen (1976), that of maximizing heterozygosity, the best direction to take in rehabilitating extinct stocks? How much variety of parental material is required?

The above are some of the questions for which answers will be needed in rehabilitation programs. It is recommended that a major research initiative in basic fish genetics and selective breeding be undertaken. Genetics, physiology, and behavior are three of the disciplines which need to be part of such an initiative.

While applauding the forward-looking research in genetics and selective breeding that has already been initiated in at least four locations in Canada, it appears now to be appropriate to examine these in detail to determine whether some consolidation or further coordination might be appropriate to more rapid progress on the basic questions before us.

Manipulating the Habitat

The kinds of damage inflicted on the quality fish production capacity of many Canadian waters has been discussed earlier in this perspective and will not be further reviewed here. Much of that damage has been expressed in terms of water quality and the science and initiatives appropriate to improvement in this area will be the subject of another in this series of studies. The timing and the extent of improvement in water quality will directly effect the timing and nature of rehabilitation initiatives. Other damage to the fish habitat has been expressed in terms of modified flow patterns, volumes and sedimentation in river systems, and in water level fluctuations in lakes which have become reservoirs for purposes other than fish production. Fisheries scientists and engineers have had considerable success in circumventing the impacts of damages through the installation of engineering works such as fishways, spawning channels, incubation boxes, etc. Extensive demands on this body of science will be characteristic of rehabilitation initiatives across Canada.

Lister (1974) presented an excellent brief review of the application of this kind of science to salmon enhancement on the west and east coasts since its beginning at Hell's Gate in 1945. His review includes the current operating costs of the installations and their capital costs at the time of construction. He included both "enhancement" and "compensatory" projects, the latter encompassing projects funded to some extent by nongovernment agencies as compensation for damage to the natural resource inflicted by their operations.

On the west coast, the Fisheries and Marine Service and the International Pacific Salmon Fisheries Commission have undertaken some 36 salmon enhancement projects since 1945. Capital investment to date has totalled $25 million, and the current operating costs of these projects approximates $1 million. The major portion of this investment has been devoted to the higher-valued sockeye, chinook, and coho salmon:

	Sockeye	Chum	Pink	Chinook & coho	Multi-species	Total
Capital cost ($ × 1000)	12,940	2,320	727	8,789	512	25,288
Operating cost ($ × 1000)	361	140	9	527	5	1,042

Operating costs including expenditures on project assessment are estimated at $172,000 annually.

Close to 80% of the capital expenditures on Pacific salmon enhancement have been made in the last decade, the major portion ($16.2 million) devoted to three projects: spawning channels for Babine Lake sockeye, and chinook and coho hatcheries at the Capilano and Quinsam rivers. The latter two projects apparently reflect the recent success achieved with hatchery propagation in the northwest United States, but they may be more properly classed as sea ranching than rehabilitation projects.

From the project descriptions listed it is clear that the most efficient investments in rehabilitation have been the fishways at Hell's Gate on the Fraser River and some other locations. At Hell's Gate an investment of $2.3 million has contributed importantly to fish landings marketed at $60 million over the last three decades. Fishways located at other locations in coastal British Columbia have also been generally successful.

Spawning channels constructed in the 1960s for sockeye, pink, and chum salmon have also produced good results. For example, initial production from the Weaver Creek, Seton Creek, and Big Qualicum spawning channels has indicated that landed values of the production from the first 1 or 2 years have exceeded the capital costs. These projects are operative in situations where natural stocks persisted, though at low levels. On the other hand, projects which relied on transplants have failed. The pink salmon transplants to Robertson Creek spawning channel in the early 1960s have not established a self-sustaining run, despite high egg-to-fry survival rates. The attempt to rehabilitate the Nanika River sockeye run, using stock from another part of the Skeena River system (Babine Lake), also failed; whereas at Pitt River the application of similar techniques, i.e. hatchery and incubation channel, with a native stock has produced an average of 54,000 sockeye-per-year to the fishery.

On the east coast all but one of the 25 projects described involve Atlantic salmon, the lone exception being the pink salmon transplant to North Harbour River, Newfoundland. Projects in the Maritime Provinces and Newfoundland have been undertaken by the respective regional divisions of the Fisheries and Marine Service. The Quebec Department of Tourism, Fish and Game has implemented all salmon enhancement projects in that province.

Capital expenditures since 1945 have totalled $5.6 million, and current operating costs approximate $1.2 million. A breakdown of the expenditures by region is given below:

	Newfoundland	Maritimes	Quebec	Total
Capital cost ($ × 1000)	1478	2335	1800	5613
Operating cost	209	656	315	1.180

The annual cost of project assessment, included in the operating cost totals, is estimated at $184,000.

The nine hatcheries in the Maritimes and Quebec account for 54% of the capital investment and 70% of the operating expenditures devoted to Atlantic salmon enhancement. These costs do not include the Mactaquac operation on the Saint John River, which is dealt with as a "compensatory" project. With the exception of the new Anse Pleureuse Station in Quebec, these hatcheries are relatively small, and were established over 35 years ago for fish rearing programs that differed greatly from today's requirements. Although new rearing facilities have been added to each hatchery in the last 20 years, the volume and quality of the available water supplies preclude the expansion of these stations to an economic scale. Plans are underway to consolidate and modernize this hatchery system so as to develop an economically sound program.

The remainder of the capital investment in Atlantic salmon rehabilitation has been devoted mainly to establishing salmon populations in river areas upstream of either natural or man-made obstructions. Positive results have been slow in coming and it appears that Atlantic salmon generally take 1–2 decades to colonize newly accessible areas.

Accordingly, the initiation of runs to these barren areas is now being aided by the combination of spawning channels and adult transplants (Newfoundland) and by the introduction of hatchery-reared juvenile salmon (Maritimes and Quebec).

In the freshwater areas of Canada there has been little accumulation of experience with the use of engineering facilities except hatcheries, in the rehabilitation of fish stocks. The difficulty that managers have encountered in establishing experimental installations has probably been related to the scattered nature of the resources, and to more subtle and long-term expression of the damage for which compensation is required. Thus the effect of drawdowns on lake trout re-

production as discussed by Martin (1955), and of irregular flow patterns in walleye spawning streams (Winterton 1975) are difficult to quantify. The long term effects of small dams and of land clearing on migratory species, Atlantic salmon, and more recently rainbow trout in the Great Lakes tributaries discussed by Christie (1972) and others, have not been corrected to the extent possible using available technique. Recent fishway installations for rainbow trout on the Saugeen and Ganaraska rivers have been successful in extending the stream habitat available for natural reproduction and rearing and have demonstrated the potential benefits to be anticipated from additional installations. Dodge (personal communication) estimates that the useful habitat available for rainbows can be more than doubled in Lake Erie and Ontario watersheds by dam removal and/or by fishway installations. Spawning channels and other flow and water level regulations are thought to have considerable potential for improving production from natural stocks. The artificial spawning beds as studied by Martin (1955) for lake trout and as attempted by J. M. Fraser (personal communication) for brook trout, and by C. R. Jorgenson (personal communication) for walleye hold promise of modest improvements at modest cost.

Very generally, it seems fair to state that the fisheries engineering science necessary to rehabilitation of fisheries in Canada is well established. Extension of the science is necessary, particularly in the freshwater area. Both application and extension will be best served by the continued close cooperation of engineers and fisheries scientists. Each new installation will be most effective if it receives their joint planning and their careful assessment effort.

Some More General Needs

Define "natural" productive capacity — This perspective defines fisheries rehabilitation as a set of programs designed to rebuild fish communities and fish stock complexes to, or close to, former levels of abundance. Those communities and levels are considered likely to have been equivalent to the full expression of the productive capacity of the individual ecosystems. They are also considered to have been, and in future to be, the kind of resource base from which relatively stable long-term harvests can be extracted. The target for an individual rehabilitation project then becomes equivalent to the "natural" productive capacity of that lake or river system, and the measure of success will be the degree to which that target is achieved. Methods for estimating the potential productive capacity of ecosystems will be necessary.

The development of methods for obtaining and testing estimates of the long-term fish production potential from lakes has attracted the attention of several scientists. Among these, the contributions of Rawson (1951; 1952; 1955; 1960), Northcote and Larkin (1956), and of Ryder (1965) are outstanding. Ryder et al. (1974) have reviewed the background papers which led to the development of the morpheodaphic index (MEI) as an estimator. They also briefly reviewed its application in management over a broad geographic range and in a number of lake types including those described in Regier et al. (1971), Henderson et al. (1973), and including the small brook trout waters used in Fraser's (1972) studies.

For streams, on the other hand, while there is considerable literature describing standing crops and harvest, I have been unable to locate an estimator or index to long-term fish productivity. Hynes (1970) reports that primary production in streams is largely dependent upon allochthonous (leaves, etc.) materials. It is generally agreed that morphological characteristics of streams, particularly the "riffle-pool" arrangements, and adequacy of "cover" strongly influence carrying capacity or standing crop (Saunders and Smith 1962a, b; White and Brynildson 1967; Hunt 1971). Several effects of sedimentation on stream carrying capacity for benthic organisms and for fish are also well documented. It would seem possible, given appropriately directed research effort, to develop an index to "natural" fish productive capacity of streams.

For lakes, the fish production potential indices now available can and should be used as first approximations of our targets in rehabilitation projects. Research designed to make these indices more precise, and to provide first approximation of the species or species group components of these total yield estimates should be strongly supported.

For rivers, research designed to develop indices to long term fish production potential should be encouraged.

Develop information systems — Financial and manpower resources have never been, and are not likely to be, adequate to provide for the prompt application of the appropriate pieces of management science to all waters on a lake-by-lake, or stock-by-stock basis at any one time. The available resources must be applied where the need is judged to be most critical and where the benefits to be derived are likely to be greatest.

Thus, for example, a choice must be made in 1977 between working on rehabilitation of a sockeye stock in the Fraser, or in the Skeena, or on a sea-ranching project involving coho in Georgia Strait. In Ontario for example, a choice must be made in 1977 between continuing the lake trout rehabilitation project in Lake Superior at the present level, or cutting that level of effort back to initiate a program in Lake Simcoe to prevent the possible collapse of the traditional fish resource base there. Decisions of this sort are made routinely of course, but all too frequently their bases are far more subjective than objective because information systems are poorly developed. Such decisions ought to be based on current intelligence concerning the status of the fish stocks, the habitat, and on client requirements. Such current intelligence is available only in the few Canadian situations where annual monitoring is already accepted as a recognized component of fish management practice.

Lake, stream, and species or stock surveys (inventory, mapping) have become a traditional and valuable component of fisheries science. Such surveys have been initiated by researchers seeking answers to questions about factors influencing distribution and/or seeking to understand competitive interaction between species; by managers who needed to know the extent of the resource they were attempting to manage; and by sectors of the public concerned about the status of their favorite stock or lake. The point-in-time information provided by the survey approach continues to be valuable, but with our new understanding of the impacts of changing stress levels, it is now recognized as an inadequate base on which to make decisions involving management initiatives.

Under ideal circumstances a manager would like to have, for each lake or stream, current information about the status of fish stocks and about appropriate habitat parameters which affect the status of fish stocks. He would also need a catalog of point levels of each habitat parameter which is critical to the continued health of the fish community. The latter kind of science is not available, but we can substitute trend-through-time data if we are willing to take management action on the basis of the curves. It is obvious also that trend-through-time data cannot be achieved for all parameters and for all waters individually, and a compromise arrangement must be found.

In the SCOL symposium (Loftus and Regier 1972), a considerable measure of success was achieved in treating salmonid communities and/or oligotrophic lakes as a "set" in identifying and studying the general effects of man-induced stresses on those fish communities. On the basis of that success, Loftus (1976) suggests that other types of lakes, perhaps those characteristically dominated by percids, by esocids, and others, may also be treated as "sets." Such an approach may also be applicable to rivers and streams. If the foregoing is accepted, then it should be within our means as fisheries agencies collectively, to achieve adequate trend-through-time data series, for selected critical parameters, in lakes and streams across Canada. These data series, against a completed inventory or mapping program, should provide current information for all waters adequate for objective management decision making.

Ontario is proceeding now in an attempt to identify lake "sets." Assessment units (Byrne and Loftus 1976) responsible for the gathering of appropriate trend-through-time data on fish communities, fish harvests, habitats, and clients, are being established on major waters and on lake "sets" across the province. The inventory or mapping program is continuing. A regionalized system to permit the conversion of assessment unit data to information available to local managers is being developed under the title of Ontario Fisheries Information System (OFIS).

Whether or not it will be possible to implement the above fisheries information system in Ontario, given current fiscal constraints, remains an open question at this time. Whether or not the conceptual framework for OFIS will prove adequate if implemented, also remains to be demonstrated. It has been presented here only as an indication of the kind of fisheries information system that is recommended for development regionally in Canada.

Take the adaptive (experimental) approach — Fisheries scientists are presently approaching rehabilitation programs with a justifiable new level of confidence. This confidence has emerged from new levels of knowledge about how to make fish culture effective; improved understanding of the responses of fish species and communities to the separate and joint effects of man-induced stresses; and the recognition of a general public attitude that is supporting water quality management programs capable of providing improved fish habitats. If this new level of confidence is justified, our past management experience, and indeed the quality of our new levels of understanding, make it clear that major new programs need to be viewed, not only as means of increasing fish stocks, but as means of testing hypotheses and extending our understanding of how the systems work.

In the preceding section the need for improved information systems as a basis for more objective management decision-making was discussed. The inadequacies of our historical information gathering arrangements have precluded the definitive testing of most management techniques presently being used. In rehabilitation programs, we will be attempting to apply, on large scales and in natural situations, hypotheses with which we feel comfortable, but which have yet to be thoroughly field tested. We will be attempting to apply on large scales, and in a variety of situations, results from small-scale, simple field experiments. If the foregoing is true, then it seems important that a few "type" situations ought to be selected for carrying forward major rehabilitation projects having in mind an explicit adaptive or experimental approach. While there are sound grounds for confidence that our rehabilitation efforts will provide positive benefits in terms of improved fish abundance, we recognize that we cannot predict in detail, and we need to learn as we go. The adaptive approach to rehabilitation will require integration of the distinctive and complementary roles of managers and researchers in careful design of plan, execution, and assessment for each major project.

Social and economic science needs — In the earlier years, perhaps to 1940, when there appeared to be lots of fish for everyone, the developing social and economic problems were even less evident to fisheries managers than were the potential limitations in the supply of fish. Recent decades have witnessed the emergence of complex social and economic problems, strongly accentuated by the diminishing supply of fish, which have led us to consider rehabilitation programs. The commercial fishing industry, formerly characterized by small, inshore, low-investment, individual enterprises, has emerged in recent decades as a complex industry which continues to embrace some of the traditional enterprises, but now includes also a highly sophisticated industrial component needing a large, stable, fish resource base on which to operate. Angling, as an opportunity for recreation, has been taken for granted by most Canadians since our pioneer days. Recreational fishing since the 1940s, however, has emerged in a sense parallel to the sophisticated industrial component of the commercial fishing industry, to the extent that it constitutes a major demand on an ever broadening resource base. In addition to these, the needs and rights of native people in terms of fish stocks have emerged recently as requiring serious attention all across Canada. No problem of supply was evident in early years of plenty, but now, when stocks are at low levels, and when all Canadians are more keenly aware of their rights, the issue must be faced.

While the demands of these client groups on the fisheries resources have intensified and expanded, so also have the demands of competitive water uses, with the result that the capacity of many waters to produce those resources has declined seriously. All these events, interacting, have served to define and emphasize the social and economic problems integral to fisheries management.

For some decades fisheries managers have recognized that their information base for decision making has been inadequate in terms of sociological and economic data components. Earlier attempts by fisheries people to develop such data have largely been abandoned and have been replaced by requests for studies by experts in these disciplines. In recent years some excellent studies, MacKenzie (1973), Pearse Bowden Economic Consultants Ltd. (1971), Sinclair (1960), Lambert (1975), and others have brought us closer to identifying the kinds of information needed, and closer to an appreciation of the complexities involved.

While there have been some excellent studies completed, there seems to have been a general reluctance or inability to implement the measures recommended or implied. Without attempting to discuss the reasons for the foregoing, it is suggested that until these difficult issues are faced squarely, and compromise solutions effected, the conflicts among resource users, and between resource users and other users of the water, will continue to confound the best efforts of fisheries people to manage a dwindling resource base. Rehabilitation programs, which could otherwise be successful, may fail in the long run for the same reason.

Sociological and economic experts must be an integral part of the team along with fisheries experts in planning and assessing rehabilitation programs.

Synthesis and communication — Most of the science of fisheries has been developed by researchers and managers who have duly reported their contributions as individuals. This process has provided for the appropriate recognition of the contributions to science by individuals and by their sponsoring agencies, and has led to a commendably rapid advance of fisheries science in general. It has also led to the creation of a fragmentary literature, in an expanding number of journals, which is neither obviously or easily

integrated. It has been suggested (Loftus 1976) that fisheries science has developed to the stage where it is now very difficult for individual scientists to be fully aware of what is known and reported. The science now seems to be at the stage where it is necessary to give special emphasis to synthesizing what is known, not only as a basis for new research initiatives, but also to provide for effective communication with and among managers for application, and also with the public for general understanding and support. Because of understandable preoccupation with matters of more immediate concern, both managers and researchers have tended to leave the responsibility for synthesis and communication to the other, a situation which has contributed to the ineffective application of available science and to a general deterioration of comfortable communications between researchers and managers.

If the foregoing generality comes close to reality, then it deserves special attention when a major initiative, such as a national fisheries rehabilitation program, is about to be launched. No such program can provide maximum benefits in return for funds and time expended in the absence of full support by all participants, researchers, managers, and clients. Full support of all participants can only be achieved on the basis of a broad understanding of the status of the science and on an appreciation of the useful role of each in the entire program.

Fortunately the generality of the above concern is no longer valid because there have been some recent examples of synthesis and effective communication in recent years. For example, the Ricker paper concerning the stock concept (Ricker 1972) appears to be the kind of synthesis which is essential to the success of programs such as salmon rehabilitation. We ought not to take it for granted, however, that all people who will be involved in salmon rehabilitation have had the opportunity to read it or to understand it. We certainly cannot assume that many managers in areas other than the west coast have recognized its implications in their management or rehabilitation programs. A major job of communications may yet be necessary, even though the synthesis has been in print for some years. Another recent exercise in the synthesis of existing but scattered science occurred in the SCOL symposium (Loftus and Regier 1972). There has been some effective communication of the inferences and implications in the freshwater area by virtue of training sessions and popular articles, but it is unlikely that people concerned with inshore, marine, and offshore fisheries have recognized the possible relevance to their problems.

The H. R. MacMillan series of fisheries lectures at the University of British Columbia, the Ricker (1975) publication concerning computation and interpretation of biological statistics of fish populations, the 1966 review of research programs concerned with methods for increasing salmon populations prepared by staff of the Fisheries and Marine Service, Pacific Biological Station, Nanaimo, and the review of salmon development techniques prepared by the Resource Development Branch of the then Department of Fisheries (1966), Vancouver, all are examples of good attempts at syntheses and/or communications. So a good start has been made.

It is recommended that the synthesis of available science, and its communication throughout research and management ranks, be recognized as an explicit responsibility of fisheries research and management people jointly. If these responsibilities are met, communications with client groups will follow, almost automatically. They will not be met, however, unless special working sessions, carefully organized around specific and appropriate topics are undertaken on a national, then regional basis.

The works of Roderick Haig-Brown and Rachael Carson are examples of the kind of communications which are effective in reaching the general public sector, as opposed to specific client groups, whose understanding and support is also essential to progress in the management of fisheries resources. A special initiative to provide this kind of communication for fisheries science is recommended.

Institutional arrangements — This subject is identified as one of the general issues requiring attention and resolution if the fisheries science now available is to be efficiently applied to fisheries rehabilitation programs, or indeed to fisheries management programs generally. Its resolution is important also to the effective prosecution of the new research required. If, in reading this heading, the reader immediately assumes that another reorganization is being suggested, be assured that something much more basic and effective than reorganization is implied.

During the current, joint Federal–Provincial effort to develop a Strategic Plan for Ontario Fisheries (SPOF), the working group identified "inadequate institutional arrangements" as a major issue to be addressed. The issue appeared to have two major elements; one reflected in legislation, the other in traditional interagency working arrangements.

The second working paper from SPOF listed 43 Federal and 39 Provincial acts which directly

or indirectly affect fish, fish habitats, and the fisheries manager's opportunity to manage fisheries. Clearly this is a matter requiring simplification and consolidation at both levels of government. The extent of fragmentation of authority and responsibility imposed by these acts, and by the several ministries involved, seems inconsistent with the direct value of the resources concerned. Coordination of goals and of available resources is difficult if not impossible under these circumstances. Regrettably, it is possible to give examples of projects, undertaken at formidable public expense by different ministries at a single government level which effectively cancel each other.

A number of "agreements" have been negotiated between Federal and Provincial governments which make explicit the responsibilities of the two agencies in the "shared" programs of fisheries research and management. Such agreements have from time to time been cancelled and/or renegotiated, and no two agreements are quite the same at present. Similarly, the support arrangements between the Federal Government, and in some instances Provincial governments, and Universities in support of research and postgraduate training in fisheries have changed through time and are presently at a seriously low level, if one can judge by the situation in Ontario. Similarly also, government policy with respect to industry support or development has been subject to change and sometimes negotiation. The foregoing is recorded simply to underline the fact that agreements do exist and that they are, to an important extent, negotiable. In the background study for the Science Council of Canada, Pimlott et al. (1971) also took note of these agreements and suggested that it might be advantageous to fisheries if they were reviewed.

If, in the case of the Federal–Provincial agreements, the objective is to achieve an appropriate division of responsibility and an appropriate total level of effort and coordination to achieve effective fisheries management, then one might conclude that none of the agreements is successful. On the east coast where the Federal Government has total responsibility, the shelf-seas stocks are considered to be under severe stress (Regier and McCracken 1975) and the inshore stocks are severely depressed (McCracken and Macdonald 1976). In Ontario, as an example of the freshwater areas, where the Province and the Federal Government have agreed on explicitly shared responsibility, a major increase in rehabilitation efforts is required for Great Lakes fish communities. On the west coast where a different kind of Federal–Provincial agreement is in place, a major rehabilitation program is considered necessary for the salmon stocks. Certainly the factors contributing to the declines in the fisheries resources across the country are largely external to the wording of the several agreements. Nevertheless, one wonders if the agreements, or institutional arrangements, have not in fact made some contribution to the problems, and more importantly, one wonders if such traditional arrangements will provide adequate frameworks within which rehabilitation of fish stocks can be achieved. P. A. Larkin expresses a concern of this sort in his personal communication "A view from Victoria," with respect to the Federal Government initiative in salmon enhancement.

Neither Federal nor Provincial governments can achieve the effective application of fisheries science without generous admixtures of social and economic information, nor can they do so in the absence of support from the public sector. The public sector is now recognized as much more complex than in earlier years when the idea seemed to be to do something for the commercial fishermen. The public sector is now recognized to include commercial fishermen, commercial tourist outfitters, commercial gear producers, recreational fishermen, resident and nonresident anglers, native peoples, nonconsumptive users, other water users, and others. All these clients live in a province, or operate from a provincial base. Under these newly recognized circumstances it seems impossible for the federal agency to execute effective fisheries management without full partnership with provincial agencies. It also is evident for these and other reasons that provincial agencies are unable to mount adequate programs without fully integrated federal support. Effective participation by expert university staff is essential in both research and training and can be constructive in policy planning as well, to both levels of government.

The current total allocations by federal and provincial fisheries agencies, and by other agencies funding fisheries related projects, must be considered impressive. From the public point of view it may look adequate, and most assuredly it is all "government" and it is all "tax dollars." From the vantage point of fisheries scientists the view might be remarkably similar if the unimportant, but traditional, agency rivalries and protectionisms could be stripped from the evaluation.

At this time, when fisheries science is capable of producing major improvements in fish abundance, and when fish stocks generally so badly need improved management, it would be a tragedy indeed if the major initiative now almost

within our grasp, were rendered ineffective because agencies are too comfortable in their traditional postures. In the SPOF exercise the scientists directly involved have explicitly shed their agency affiliations and have been able to communicate effectively and to plan for fisheries rather than for fisheries agencies. It will be interesting to see if governments can do likewise.

Summary and Recommendations

A brief review of the status of salmonid communities on the west and east coasts, and of fish communities in selected freshwater lakes is presented. Most fisheries are presently operating on resource bases which are depressed by about half in comparison to earlier abundance levels. Many discrete stocks which formerly contributed to the resource base are at critically low levels, and some are extinct.

Stresses contributing to the currently depressed stock levels differ mainly in degree from one coast to the other and include: (1) overexploitation — evident in all areas considered. Fishing power and demands by client groups continue to increase; (2) excessive nutrient loading — evident in waters adjacent to metropolitan areas, intensive agriculture; and excessive cottage and recreational development; (3) contaminant loading — evident in waters adjacent to intensive industrial, mining, forestry, and agricultural developments; (4) modified flow patterns — resulting from natural events, but mainly from engineering works such as dams and diversions which impede access to spawning areas and which reduce or modify the fish production capacity of streams or lakes ; (5) new species invasions, such as sea lamprey, smelt, and alewives; (6) shoreline modification, irrigation, etc.

The stock concept, as explicitly recognized in sockeye salmon and other salmonids on the west coast, is seen as applicable to most other important fish species.

Major thrusts, such as those currently being initiated for salmon on the west coast to regain former levels of fish abundance, are timely now. Much of the science needed is available but requires synthesis and transfer. The new science required can be identified and seems within reach. Some initiatives in water quality and habitat management which are prerequisites for fisheries rehabilitation are already under way. Examples include the programs of the Great Lakes Fishery Commission and of the International Joint Commission.

The term "enhancement," despite its current popularity, is rejected on the grounds that it encompasses two quite different, and perhaps antagonistic, approaches to improving the abundance of fish: sea ranching and rehabilitation. The consequences of taking one or the other approach are here seen to be quite different and to require explicit policy decisions. The author recommends the rehabilitation approach for Canada, discusses science needs in that context, and makes the following recommendations:

1) Extend the application of available science concerning salmonid hatching, rearing, and planting in Canada by modernizing fish culture facilities and by recognizing fish culture as a profession. Arrange for the assimilation of the fish culture science developed elsewhere for other species such as walleye and coregonids, and further develop this science.

2) Give special emphasis to the stock concept in rehabilitation programs. This emphasis may require the development of small, versatile, and mobile fish culture units rather than the more "efficient" large, permanent, fish culture stations now popular.

3) Develop a national center or centers for fish health (diseases and parasites) work. A considerable research initiative will be needed, along with diagnostic and prophylactic services for government and for private sector fish culture operations. Federal, provincial, and university people staffing the facility should be fully integrated. Discourage the careless transfer of fish.

4) Develop a national center or centers for fish nutrition studies, having terms of reference similar to those listed for (3), and preferably integrated with the location for (3).

5) Sponsor a major basic research initiative in fish genetics and selective breeding. Physiologists and behaviorists as well as geneticists will be needed as part of the team. Review the current scattered initiatives in this field with a view to consolidating available experts in a national center or centers. Here too, federal, provincial, and university staffs should be integrated.

6) Continue research and management studies (gear selectivity, stock in relation to community ecology) designed to improve the capability to harvest stocks selectively.

7) Extend fisheries engineering science by team planning and assessment on a project-by-project basis on the coasts. Initiate programs to adapt the available science to freshwater species.

8) Provide support for additional research designed to refine indices to fish production potential for lakes and streams. Encourage the use of available indices as being first estimates of the targets for rehabilitation projects.

9) Develop fisheries information systems on a

regional basis. Such systems should provide continuing data series (fish community, harvest, habitat, and users) from carefully selected type waters, and will help managers decide what should be done where, and when. Fish community as used here has reference to the several species in the community and to the several stocks within species. Resource mapping (surveys) should be continued to completion.

10) Social and economic data, now more important than ever in management decision making, must be greatly expanded and incorporated in the "user" component of fisheries information systems.

11) Take the adaptive (experimental) approach to a few large rehabilitation projects. While we have confidence in our ability to improve standing crops, it is recognized that we cannot predict in detail the consequences of our efforts. Teams of research and management people must be integrated at all stages of planning, execution, and assessment so that learning opportunities will be maximized.

12) Explicit efforts are needed to synthesize the scattered and voluminous science that is available. We will probably find that more is known than we have been aware of. Such syntheses will provide a necessary means of organizing for more effective communications among fisheries people and with the public.

13) The traditional institutional arrangements for getting the job of fisheries research and management done have not been very successful. The distinction between federal, provincial, or university experts is of little importance to people who foot the bill. Perhaps in approaching a major new initiative in fisheries we have a unique opportunity to forget our traditional differences, and to do, collectively, a much more effective job.

14) Brief comment, specific to B.C. salmon, may be appropriate on the eve of the major initiative currently being planned. While all of the above recommendations have some application to salmon rehabilitation, particular emphasis is suggested for (a) the policy decision relating to rehabilitation vs. sea ranching and (b) the adaptive or experimental approach. The time is right for an aggressive initiative. That initiative should be undertaken in a few carefully selected sites, and it should be very carefully planned by the best team of experts available in research and management. That team must also be applied in the follow-up assessment studies which will be critical to the continued success of the salmon program, and to programs across the country. Because the demands on research will be extensive, both for specific research initiatives and for participation in field projects, the percentage of available operating funds designated for research will need to be high, perhaps 15 or 20%, particularly in the first 10 or 15 years.

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Chlorinated Guaiacols in Bleachery Wastes: Comments on a Paper by Leach and Thakore

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ROGERS, I. H. 1976. Chlorinated guaiacols in bleachery wastes: comments on a paper by Leach and Thakore. J. Fish. Res. Board Can. 33: 1858–1860.

Tri- and tetrachloroguaiacol are constituents of kraft bleachery wastes which are acutely toxic to salmonids. There are four possible structural isomers of trichloroguaiacol and no evidence was presented by Leach and Thakore to support their claim that the compound they found had the 3,4,5 substitution pattern. Details as to how the authors synthesized their standard chlorinated guaiacols were not presented. Identification of chlorinated resin acids and epoxides derived from unsaturated fatty acids is considered to indicate poor pulp washing efficiency and we have not observed such compounds in caustic extraction effluents from mills we have studied.

ROGERS, I. H. 1976. Chlorinated guaiacols in bleachery wastes: comments on a paper by Leach and Thakore. J. Fish. Res. Board Can. 33: 1858–1860.

Le tri- et le tétrachlorogaïacol sont des constituants de déchets de blanchisserie de papier kraft d'une toxicité aiguë pour les salmonidés. Il y a quatre isomères structuraux possibles du trichlorogaïacol, et Leach et Thakore ne donnent pas de preuve à l'appui de leur prétention que le composé qu'ils ont trouvé possédait le schéma de subsitution 3,4,5. Ces auteurs n'expliquent pas en détails la façon dont ils ont synthétisé leurs gaïacols chlorés étalons. La présence d'acides résineux chlorés et d'époxydes dérivés d'acides gras insaturés est considérée comme signe d'un lavage inefficace, et nous n'avons pas observé de tels composés dans les effluents d'extraction caustique des moulins que nous avons observés.

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A paper entitled "Isolation and identification of constituents toxic to juvenile rainbow trout (*Salmo gairdneri*) in caustic extraction effluents from kraft pulpmill bleach plants" was published in the August 1975 issue of this journal and requires comment regarding a number of technical inaccuracies. The work was performed by J. M. Leach and A. N. Thakore (1975) at B.C. Research under contract to the Committee for Pollution Abatement Research (CPAR).

In collaboration with Dr L. H. Keith of the Southeast Environmental Research Laboratory, U.S. Environmental Protection Agency, Athens, Ga., I had been involved in studying the nature of some acutely toxic compounds present in bleachery wastes from two mills in British Columbia commencing in August 1973. Our results, identifying two chlorinated guaiacols, were published in October 1974 (Rogers and Keith 1974). The following month I identified these compounds in a paper presented at an industry workshop (Rogers 1974). Because we used gas chromatography to analyze for these compounds, it was necessary to methylate the bleachery waste extracts with diazomethane which converts free phenolic hydroxyl groups to their corresponding methyl ethers. We therefore identified our compounds as 3,4,5-trichloroveratrole and 3,4,5,6-tetrachloroveratrole and proved that the precursors in the bleachery wastes were guaiacols and not catechols. This work is now in press (Rogers and Keith 1976).

Let me now explain the technical points on which I criticize the work by Leach and Thakore, which was submitted to the *Journal* in January 1975.

The authors inform the reader that 3,4,5-tri-

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chloroguaiacol was "prepared from guaiacol using conditions similar to those described by Sarkanen and Dence (1960)." Consultation of this reference reveals that trichloroguaiacol was not reported by these authors. However, Sarkanen and Dence did include a reference to some French workers (Fort et al. 1955) who had reported the synthesis of 4,5,6-trichloroguaiacol by the chlorination of guaiacol in acetic acid solution. This, the most relevant paper on the synthesis of chlorinated guaiacols, was not mentioned by Leach and Thakore.

Likewise, the reader is referred to Sarkanen and Dence (1960) for details on the synthesis of 3,4,5,6-tetrachloroguaiacol from guaiacol. Consultation of the reference shows that indeed these previous workers did prepare tetrachloroguaiacol, but they started from vanillyl alcohol, not guaiacol.

It is necessary here to discuss the problem of the structural isomers of trichloroguaiacol (tcg). There are in fact four possible structures as shown in Fig. 1. After methylation with diazomethane, for purposes of analysis by gas chromatography, only two structures for trichloroveratrole (tcv) are possible.

Arguments based on NMR spectral properties of the trichloroveratrole, isolated by Dr Keith from a methylated extract of bleach plant effluent, convinced us that we had found the 3,4,5-isomer and not the 3,4,6-analogue. This has recently been confirmed using Fourier-transform IR spectroscopy and carbon-13 NMR spectrometry (I. H. Rogers unpublished data). However, the precursor of this compound may have been either 3,4,5-tcg or 4,5,6-tcg. Despite access to some of the most powerful chemical instrumentation available in modern science, we are still unable to decide which isomer predominates in bleachery wastes and have so far been successful in synthesizing only one of the two possible precursors of 3,4,5-tcv. It was therefore an error that I reported in an abstract for a discussion (Rogers 1974) that our work had identified 3,4,5-tcg as the precursor in bleachery waste. To the best of my knowledge nobody has ever reported the synthesis of this substance. How then did Leach and Thakore deduce that their trichloroguaiacol had this structure when they advanced no evidence at all on the question? Their reference to Heilbron and Bunbury (1953) is most ambiguous in that this chemical dictionary refers back to three papers published around the turn of the century before modern analytical techniques became available. Two melting points are given for two monomethyl ether derivatives of trichlorocatechol, but the citation is vague, as it does not specify which

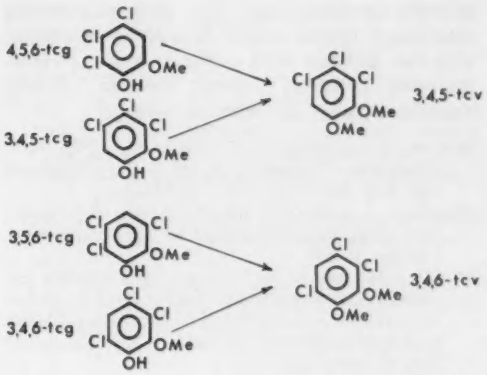

FIG. 1. Four possible structures of trichloroguaiacol.

melting point goes with which derivative. These early papers were reviewed by the later French workers (Fort et al. 1955).

We have measured concentrations in the range 0.24–0.63 mg/liter of tcg and 0.043–0.140 mg/liter of tetrachloroguaiacol in six samples of caustic extraction effluent taken on 6 consecutive days at a Vancouver Island mill. We found 96-h LC50 values of 1.10 and 0.44 mg/liter, respectively, in tests against sockeye salmon (*Oncorhynchus nerka*). Typically caustic extraction effluent from this mill kills salmon after dilution to 10% of its original concentration. Dr Keith and I were therefore unable to explain the toxicity of the mill waste samples, as only trace quantities of toxic resin acids were detectable with the aid of a gas chromatograph–mass spectrometer–computer system. No other chlorinated species were detected by us in bleachery wastes from two mills that we studied. A number of nonacutely toxic saturated fatty acids and two long-chain hydrocarbons were identified (Rogers and Keith 1974). Scanning of the mass spectral data shows that the other three compounds described by Leach and Thakore were not present in our samples. Indeed there is no reason to expect significant amounts of any of these three compounds in bleachery effluent at a mill with an efficient pulp washing system, because only trace amounts of resin and fatty acids are then carried into the chlorination stage with the incoming brown stock.

In summary, I state that the paper published in the August issue of the *Journal* is carelessly written and misleading in its implications. From my own research experience in this field, I believe the major contribution to the toxicity of caustic extraction effluent comes either from chlorinated lignin residues of too high a molecular weight to be discerned by gas chromatographic

analysis, or from many low molecular weight chlorinated species which decompose in contact with hot stainless steel surfaces in gas chromatographic columns. Current Swedish research strongly supports the latter conclusion.

FORT, R., J. SLEZIONA, AND L. DENIVELLE. 1955. Sur la chloruration du gaiacol: les tri- et tetrachloro-gaiacols. Bull. Soc. Chim. France p. 810–815.

HEILBRON, I., AND H. M. BUNBURY. [ed.] 1953. Dictionary of organic compounds. Eyre and Spottiswoode, London. 4: 560 p.

LEACH, J. M., AND A. N. THAKORE. 1975. Isolation and identification of constituents toxic to juvenile rainbow trout (*Salmo gairdneri*) in caustic extraction effluents from kraft pulpmill bleach plants. J. Fish. Res. Board Can. 32: 1249–1257.

ROGERS, I. H. 1974. Toxic factors in bleached kraft mill effluents. Abstracts to presentations at the 1974 NCASI west coast regional meeting, Portland, Oregon, November 12.

ROGERS, I. H., AND L. H. KEITH. 1974. Organochlorine compounds in kraft bleaching wastes. Identification of two chlorinated guaiacols. Fish. Mar. Serv. Res. Dev. Tech. Rep. 465: 21 p.

1976. Two chlorinated guaiacols identified in toxic kraft bleachery effluents. Proc. of the environmental chemistry division of the First Chemical Congress of the North American Continent, Mexico City, Mexico, Nov. 30–Dec. 5. (In press)

SARKANEN, K. V., AND C. W. DENCE. 1960. Reactions of p-hydroxybenzyl alcohol derivatives and their methyl ethers with molecular chlorine. J. Org. Chem. 25: 715–720.

Response to the Comments of I. H. Rogers

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LEACH, J. M., AND A. N. THAKORE. 1976. Response to the comments of I. H. Rogers. J. Fish. Res. Board Can. 33: 1860–1861.

Rogers' rodomontade ignores the facts. Compounds named in our paper are widespread and important toxic constituents of caustic extraction effluents from kraft pulpmill bleach plants.

LEACH, J. M., AND A. N. THAKORE. 1976. Response to the comments of I. H. Rogers. J. Fish. Res. Board Can. 33: 1860–1861.

Dans sa rodomontade, Rogers ne tient aucun compte des faits. Les composés mentionnés dans notre article sont largement répandus et sont d'importants constituants toxiques des effluents d'extraction caustique de blanchisseries de papeteries kraft.

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COMMENTS made by Rogers are based primarily on conjecture, and do not merit a detailed response. Results in our paper were from studies of seven kraft pulpmills in western Canada (Leach and Thakore 1975a). We have now examined caustic extraction effluents from the bleach plants at a total of 16 mills across Canada and in the United States (Leach and Thakore 1975b, 1976). Our conclusion remains that 3,4,5-trichloro- and 3,4,5,6-tetrachloroguaiacol, monochloro- and dichlorodehydroabietic acid, and 9,10-epoxystearic acid are important toxic factors for fish in this waste stream. Chemical fractionation procedures leading to isolation of the compounds in pure form were monitored at all stages by acute lethal bioassays using juvenile rainbow trout (*Salmo gairdneri*). Our more recent studies show that 9,10-dichlorostearic acid, 4,5,6-trichloroguaiacol, and alkylphenoxypoly(ethyleneoxy)ethanol pitch dispersants also contribute to the toxicity of caustic extraction effluents at some mills (Leach and Thakore 1975b, 1976). High molecular weight lignin residues may impart toxicity to chlorination-stage bleach plant wastes, but the toxic contribution of such materials to the caustic extraction stream appears to be at most a minor one (Leach and Thakore 1976).

We are pleased that Rogers has made progress towards the identification of 3,4,5-trichloroguai-

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acol; C^{13} NMR spectroscopy is in fact an excellent technique for interpreting the substitution patterns of chlorinated guaiacols (A. C. Oehlschlager and A. N. Thakore unpublished data). However, it is remarkable that "despite access to some of the most powerful chemical instrumentation available in modern science," Rogers cannot detect toxic constituents which in many cases are present at concentrations of 5–10 mg/liter in caustic extraction effluents (Leach and Thakore 1976).

We shall await with interest the time when Rogers feels able to document his "beliefs" in a manuscript for scrutiny by referees. The tone of the text hopefully will be less offensive than his Letter to the Editor.

LEACH, J. M., AND A. N. THAKORE. 1975a. Isolation and identification of constituents toxic to juvenile rainbow trout (*Salmo gairdneri*) in caustic extraction effluents from kraft pulpmill bleach plants. J. Fish. Res. Board Can. 32: 1249–1257.

1975b. Identification of the toxic constituents in kraft mill bleach plant effluents. Can. For. Serv., CPAR Rep. 245-2: 76 p.

1976. Identification of the toxic constituents in kraft mill bleach plant effluents. Can. For. Serv., CPAR Rep. 245-3: 93 p.

Discussion of Benthic Aspects of "Perspectives" November 1975

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ELLIS, D. V. 1976. Discussion of benthic aspects of "Perspectives" November 1975. J. Fish. Res. Board Can. 33: 1861–1863.

Some of the recommendations in the "Perspectives" of November 1975 concerning benthos investigations are not new but have been attempted over the past 20 years without gaining more than token institutional support. Accurate species identification services undoubtedly are needed by the oceanographic community but emphasis should also be given to rational decision-making on what species should be identified. In this context, use by government agencies of contract arrangements for obtaining biological services has not yet been matched by development of appropriate procedures for quality control of the end product.

ELLIS, D. V. 1976. Discussion of benthic aspects of "Perspectives" November 1975. J. Fish. Res. Board Can. 33: 1861–1863.

Quelques-unes des recommandations mises de l'avant dans « Perspectives » de novembre 1975 concernant les recherches sur le benthos ne sont pas nouvelles : on a tenté de les réaliser au cours des 20 dernières années sans obtenir plus qu'un appui institutionnel symbolique. La communauté océanographique a sans doute besoin de services d'identification précise des espèces, mais il faut également se préoccuper d'un processus rationel de décision quant aux espèces à identifier. Dans ce contexte, les procédures contractuelles utilisées par les organismes gouvernementaux dans le but d'obtenir des services biologiques n'ont pas encore été accompagnés d'un développement de procédures appropriées pour le contrôle de la qualité du produit final.

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THIS Discussion concerns benthic aspects of the tripartite "Perspectives" on biological oceanography in Canada: "Biological Oceanography in Canada: A Perspective and Review" by T. R. Parsons; Appendix I "A Prognosis for Canadian Benthic Biological Oceanography" by B. T. Hargrave and C. D. Levings; Appendix II "Biological Oceanography in Canadian Arctic and Subarctic Waters" by M. J. Dunbar. It provides further information supporting the actions recommended, suggests some extensions of needs, and presents a few minor corrections and differences of opinion. It notes, however, that the calls for action are not new, but have been made before during the 1950s and 1960s by the few benthic

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biologists then attempting to market their skills and awareness of problems to scientific agencies of the time.

The three papers in the "Perspectives" essentially recommend the following actions: 1. new technological approaches to benthic studies; 2. greater cooperation between benthic biologists to answer important questions nowadays posed by developments in ecosystem theory and concepts; and 3. adequate taxonomic studies and identification services.

The prime technological call is for a properly equipped submerged sampling platform, either mobile for surveys (a submarine) or stationary for detailed investigations (a habitat). This is based on dissatisfaction with the basic sampling gear now in use, and the simplistic attempts to resolve their disadvantages by submersibles. There are, however, other possibilities for technological development including side-scanning and sediment-profiling sonars, camera–grab combinations, simulated benthic communities in laboratory facilities such as the aquatron at Dalhousie University, and computer modelling of community variability based on the time-series data recently available at least from the Pacific coast. This discussant knows of grant applications during the mid-1960s to develop use of the first two sets of instruments for specific purposes, the latter even for abyssal studies at Weather Station P (see the suggestion by Parsons). Computerized data processing of survey data was under development as early as 1966 on the west coast at the Nanaimo Biological Station (Bernard 1967) and the University of Victoria (Ellis 1968). Preliminary discussions at that time to interface and extend the two systems to a national network lapsed through lack of institutional interest. Implementation then would have meant that we would now have almost a decade of tapebanked environmental–biological data for hundreds of species.

The call for greater cooperation between benthic biologists due to the need to understand involvement of such specialized ecosystems as the sediment–water interface on productivity of bottom-feeding fish and mammals raises the hope that appropriate funds may now become available for cooperative projects. I am tempted to add "at last," if only because of the following rather extreme example. In 1957 the Arctic Unit of the Fisheries Research Board had to file away a report on the contents of 135 walrus stomachs, and their indications of walrus–sediment bank relationships, because of lack of opportunity for the cooperative project between mammal and benthic biologist to progress further. In 1975, 18 years later, when a need arose to document walrus feeding habits in arctic Canada in order to predict impact of a mine-tailing discharge to the sea, the only data available were still the filed-away 1957 report. In contrast, an example of good cooperation and teamwork comes from the integrated series of papers on benthic productivity and metabolism, community structure, and the taxonomy and biology of individual benthic species from the Department of Oceanography, University of Washington, based on studies just south of the U.S.–Canadian border. It is essential for Pacific coast benthic biologists to be familiar with the University of Washington benthic program for lack of a comparable Canadian contribution.

All three papers in the "Perspectives" comment on the need for accurate taxonomic and identification services, and this classical requirement in biology is even more urgently needed now than in the past due to the large expenditures for research on little known organisms. It has been this discussant's experience that many thousand, even hundreds of thousand dollars have been spent equipping and operating chemical laboratories for such analyses as heavy metals in biological tissues, but the organisms being tested have been identified to an almost unbelievably elementary level. With well-known species variability in accumulative capacity for metals and organics, much sophisticated chemical testing is unsophisticated, to say the least, in biological terms. It is not through specialist pride alone that taxonomists have traditionally refused to accept species identifications outside their own journals.

The difficulties in obtaining accurate species identifications will not be resolved, however, by simply extending the scope of services such as those provided by the Canadian Oceanographic Identification Centre, desirable though this extension is. Some conceptual and technological development is also needed and more rigorous technical training of the student identifier. Ultimately computerized matching systems comparable to disease diagnosis will be developed, but for the moment even use of punch card systems and application of xeroxing to original species and generic descriptions would be an improvement on the widespread over-reliance on keys. Keys are developed largely by and for specialists, and when used by identifiers with no experience in taxonomy are liable to be misleading. They cannot be considered accurate scientific instruments without frequent calibration against species descriptions.

More important than improving identification procedures is the need to develop rational criteria in deciding which organisms to identify to species level in benthic surveys, rather than following

present subjective practices of choosing arbitrarily, for logistic reasons, or personal convenience, or conversely attempting to identify all organisms (usually with accuracy varying between phyla). Biologists interested in benthic energetics and biogeochemical cycling undoubtedly need a facility to identify their species accurately, so that their replicated experiments are run on the same species, but biologists interested in community structure (to use Hargrave and Levings categories) need to know which of many hundred or even thousand organisms are sufficiently important ecologically that they merit species identification. Fisheries and pollution biologists, etc., need both types of help. Once again there is an argument for cooperation and teamwork.

Identification procedures raises a question touched upon by Dunbar: the "make or buy" policy of government mediated through contracts to biological and environmental contractors. Species identifications require professional or technical personnel, an adequate laboratory, and especially library and reference collections of specialist-identified specimens. These are time-consuming and difficult to acquire, and hence are expensive services. Cost-benefits in terms of identification levels required should be calculated carefully by a government client for any sorting and identification contracts. The "make or buy" policy has fostered development of biological and environmental contractors with varying facilities and degrees of expertise, but, in contrast, government (and also industrial) clients are only just developing a complementary set of procedures to provide continuing quality control of the product. A further problem arises from such contract science, whether given out by government or industry, in that many surveys based on contracts remain "confidential." A substantial body of "confidential" reports now exists in government and industry files. These have usually not been subjected to peer appraisal in the manner of scientific manuscripts submitted for publication to professional journals. Every now and then they emerge to public view in the sense that nonpeer-appraised conclusions are quoted by those who just happen to know the right files. Developments are needed to handle problems such as these, and the answer appears to lie in thorough and continuing "in-house" or independent supervision and appraisal of contract reports. A safeguard for contract product quality would be for government clients to designate a staff scientist to carry personal responsibility through being named as joint author with the contractor. This would encourage government to develop a "clerk of the works" capability in biological contracts and would combine the best aspects of personal responsibility as evolved by the engineering and scientific professions.

Finally a few statements in the thought-provoking November "Perspectives" should be corrected or at least modified. The earliest benthic investigations in Canada were some time prior to 1819 during the first arctic expedition led by Captain J. C. Ross (1819). Indeed he claims to have invented a "deep sea clamm" apparently similar to the quantitative grabs now widely in use. Some arctic marine data is available from the winter 1954–55 (Ellis 1960). Parsons' objection to benthic grabs as sampling devices is too simplistic. Admittedly grabs have faults, but the technology and operation of grabbing is more sophisticated than given credit for by Parsons, and there is a body of critical literature available to those wishing to learn the techniques (see Holme and McIntyre 1971). Appropriate use of several instruments, and good sampling design based on a variety of available numerical analytical procedures can do much to overcome the problems of interpreting grab samples.

BERNARD, F. R. 1967. British Columbia marine faunistic survey. Numerical codes for Mollusca. Fish. Res. Board Can. MS. Rep. 914: 30 p.

ELLIS, D. V. 1960. Marine infaunal benthos in arctic North America. Arct. Inst. North Am. Tech. Pap. 5: 53 p.

1968. A series of computer programs for summarising data from quantitative benthic investigations. J. Fish. Res. Board Can. 25: 1737–1738.

HOLME, N. A., AND A. D. MCINTYRE. 1971. Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford and Edinburgh. IBP Handb. 16: 323 p.

ROSS, J. C. 1819. A voyage of discovery made under the orders of the admiralty in His Majesty's ships Isabella and Alexander for the purpose of exploring Baffin Bay and enquiring into the probability of a north-west passage. John Murray, (Publishers), Ltd., London. 252 p.

Reply to D. V. Ellis's Comments on a Prognosis for Canadian Benthic Biological Oceanography

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LEVINGS, C. D. 1976. Reply to D. V. Ellis's comments on a prognosis for Canadian benthic biological oceanography. J. Fish. Res. Board Can. 33: 1864.

A reply to Dr Ellis's comments on a prognosis for Canadian benthic biological oceanography is presented. Selection of species to identify from benthic communities poses fundamental ecological questions, e.g. why are some species common and others rare? Answers are not immediately forthcoming and site-specific studies are necessary for applied work. To provide a basis for empirical studies, keys and checklists are required.

LEVINGS, C. D. 1976. Reply to D. V. Ellis's comments on a prognosis for Canadian benthic biological oceanography. J. Fish. Res. Board Can. 33: 1864.

Ce qui suit est une réponse aux commentaires de M. Ellis concernant un pronostic pour l'océanographie biologique benthique au Canada. Le choix des espèces à identifier dans les communautés benthiques soulève des questions écologiques fondamentales, e.g. pourquoi certaines espèces sont communes et d'autres sont rares? Il n'y a pas de réponses immédiates et les travaux d'application doivent être précédés d'études sur des sites spécifiques. Des clés et des listes de distribution sont nécessaires comme base d'études empiriques.

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DR ELLIS has raised a number of interesting issues, two of which I would like to respond to.

The quandary of which species (benthic or otherwise) to identify broaches some fundamental ecological questions. The questions depend on the particular hypothesis an investigator wishes to test but include the following: 1) how valid is the concept of "keystone species" as developed by Paine (1966)? 2) how valid is the concept of indicator species? 3) why are some species common and others rare? A variety of theoretical attacks on these problems are necessary; breakthroughs with application to benthic studies may occur in a number of fields of ecology.

The grand paradigm of benthic ecology, which will enable us to throw away our keys, has yet to appear (see also Mills 1975). Since empirical, state-of-the-art science is required at present, special care must be taken to avoid undermining or downgrading present efforts directed toward the development of identification guides for marine benthic organisms found in Canadian waters. Future research efforts to improve prediction must strike a balance between structural and functional approaches, but this will only be possible in a variety of ecosystems when the taxonomic homework is done. An evaluation of samples, specimens, and knowledge presently available is required. In applied work, museum personnel (e.g. regional COIC representatives in concert with other experts) should be actively playing "police persons" in taxonomic matters, so that keys can be frequently calibrated for scientific or legal purposes.

MILLS, E. L. 1975. Benthic organisms and the structure of marine ecosystems. J. Fish. Res. Board Can. 32: 1657–1663.

PAINE, R. 1966. Food web complexity and species diversity. Am. Nat. 100: 65–75.

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Heavy Metals in the Aquatic Environment. An international conference. *Edited by P. A. Krenkel. Pergamon Press, Inc., Oxford, England, 1975. x + 352 p. $50.00. U.S.*

This book is the proceedings of an international conference on heavy metals held in Nashville, Tennessee in December 1973. In the preface P. A. Krenkel stated that the conference was "directed towards the attainment of a rational approach towards the control of heavy metals in the aquatic environment." He felt that regulatory agencies were applying overly stringent and arbitrary standards for metals and implied that the proceedings would provide scientifically sound statements about heavy metal effects on biota, movements and distribution in aquatic ecosystems, plus suggestions for realistic standards and controls. A very clear picture of the human health effects of mercury from aquatic ecosystems was given by detailed examination of dose–response relationships, movements of mercury from sources to sediments, methylation in the sediments, and transfer through fish to man. There is adequate material to justify controls on mercury discharges and to predict the extent of contamination by known mercury sources. Several authors criticize the Japanese, Canadian, and United States governments for not taking stronger action to limit discharges and to protect consumers of contaminated fish.

The human health effects of cadmium are reviewed less extensively than mercury and there is little information on other metals.

The effects of metals on the health of aquatic organisms rated only one fragmentary review. The author repeated at length the complaint that water quality standards for heavy metals are set without informed judgements. Subsequently, he presented brief analyses of a few studies of lethal and sublethal effects of metals on aquatic biota. This small sample of the available information did not provide any perspective. For example, after reading that "changes in the blood picture of brown bullhead result from exposure to low level concentrations of copper," I could not assess whether these concentrations would affect brown bullhead populations or the success of a bullhead commercial or sports fishery. A more useful discussion would review the ecological impact of acute lethal and chronic sublethal exposures, the potential for each, the metals that are most frequently discharged, the lowest concentrations that would produce a harmful effect on aquatic biota, and the factors that affect toxicity.

Except for mercury, there was no comprehensive overview of the movements of metals from their source to their eventual sink in aquatic ecosystems. While the papers on metals transport were authoritative, they were limited to a few subjects. For example, a paper entitled "The accumulation and excretion of heavy metals in organisms" described the distribution in humans of mercury and cadmium absorbed from food. A small amount of data was given for lead. Accumulation of mercury and cadmium by aquatic biota from their food was considered briefly but accumulation directly from water was not. With the exception of an excellent paper by G. F. Lee on hydrous metal oxides, the occurrence and measurement of various metal forms in water was ignored. This was disappointing since the chemical forms of a given metal affects its toxicity to aquatic organisms. The distribution of metals in fresh water among particulate and soluble complexes was another issue inadequately covered. Analytical techniques for total mercury and methylmercury were well described and there was one paper for total analyses of metals other than mercury.

Papers on source reduction methodology described the current technology for removing heavy metals from water. It is rather disturbing that, since the application of "best practical technology" to limit mercury discharges, over 50% of mercury used in chlor alkali plants is still unaccounted for. This equalled about 23 tons in Canada during 1972.

Possible corrective measures for mercury contamination of lake sediments were proposed by several authors. Most of these ideas appeared rather impractical and, according to one discussant, would only accentuate the problem. The effects on benthic ecosystems of proposed large-scale environmental manipulation were not considered.

The final paper in the volume deals with "benefit–risk" analyses, a process whereby decisions on use of heavy metals can be made by a systematic balancing of economic benefits and environmental risks. As described, the method required statistical

estimations of benefits and risks. While there is adequate information for economic benefits, the opposite is true for environmental risks. The author clearly indicates a need for realistic statistical appraisals of environmental impacts.

The editing of this book was rather patchy. Some authors continually switched from one terminology to another without definitions and data were often compared using different units. Laitinen and Skogerboe used a nonstandard bibliography format and De Groot and Allersma confused me with "Lake Ijssel," "Yssel Lake," "River Yssel," and "distributary Ijssel." Jonasson and Timperley spoke of "genetic relationships" among metals, while Wood included among sources of metals, "natural Bio-leaks (e.g. volcano eruptions, etc.)." I was also surprised to see included a paper describing a study plan for a future field survey, and a paper that consisted only of an uninformative abstract.

In summary, the preface of this book suggested that the presentations provided a scientific basis for water quality standards for heavy metals. For the human health aspects of mercury, adequate information was presented, but it requires a good synthesis to be really useful. For other metals, and for impacts on fisheries, there is not enough material to even consider standards. Consequently, this book will be most useful to those scientists studying mercury who require a review of the literature to 1973. In view of the $50 price tag, I would recommend this book for purchase only by libraries.

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Statistical Calculations — How to solve statistical problems. *E. Joe Middlebrooks. Ann Arbor Science Publishers, Ann Arbor, Mich. 1976. viii + 120 p. $12.50.*

This is not a book for a statistician. It is too restrictive, too basic for those whose business it is to explore the realms of probability and likelihood, but therein lies its value. The rapid rise of accessibility to large computers with systems of statistical analyses and the ubiquitous, rechargeable, programmable hand calculator have placed statistical analysis in the hands of every man. Unfortunately, the brute can bite the hand that holds him. This book is designed for the researchers, secure in their own fields, who, forced by editors who assume that "significant" is always spelled with a following bracket and some "p" value, seek help beyond their understanding, memory, or need. To the reader confronted by pages of computer output or worse still a single illuminated answer, this book becomes a most useful guide and companion. The step-by-step examples, all easily verified with paper and pencil, make understanding of the processes used clear and logical. The presentation shows not only what was done but why, and leads the reader to conclusions that become obvious. This is the book's prime value. As familiarity increases, especially for those who have forgotten even the name of their statistics professor, the secondary value emerges. Diligent examination of the well-chosen examples will lead to the choice of the appropriate analysis for the work in hand. In fact, such examination may well point to new and unimagined analyses. and with increasing familiarity to areas beyond the scope of this slim volume. The chapter (or exercise as the author calls it) on randomized complete block design particularly appealed as did the discussions on confidence limits in linear and nonlinear regression. Personal preference would have wished for an example of functional regression but this perhaps is not the appropriate medium. It is a pity that the book is not available in soft cover at a cheaper price. Its message is important enough to deserve a wide audience but its price, which approaches that of its prime reference (Steele and Torrie), will tend to discourage its acceptance.

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CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 31, No. 6 — paper by R. H. Payne: *Transferrin variation in North American populations of the Atlantic salmon, Salmo salar.*

Page 1038: Left column, par. 6, line 10 should read "of buffered ferric chloride solution: 50 ml of 0.02 M".

VOLUME 32, No. 8 — paper by T. K. Pitt: *Changes in abundance and certain biological characteristics of Grand Bank American plaice, Hippoglossoides platessoides.*

Page 1385: Left column, par. 6, line 3 should read "$C_n = \frac{F}{Z_n}(1 - e^{-Z_n})N_n$." Right column, par. 3, line 9 should read "and $C_{n+1} = E_{n+1}(1 - e^{-Z_{n+1}})N_{n+1}$"; line 10 should read "but $N_{n+1} = N_n e^{-Z_n}$"; line 13 should read $\frac{C_{n+1}}{C_n E_{n+1}(1 - e^{-Z_{n+1}})} = \frac{e^{-Z_n}}{E_n(1 - e^{-Z_n})}$; line 15 should read "starting exploitation rate ($E_{n+1}(1 - e^{-Z_{n+1}})$) for the."

Page 1391: Table 2, "to" should be "t_o."

VOLUME 32, No. 9 — paper by C. P. Archibald: *Experimental observations on the effects of predation by goldfish (Carassius auratus) on the zooplankton of a small saline lake.*

Page 1590: Left column, par. 1, line 3, "2.05 m on a side" should read "3.05 m on a side."

VOLUME 32, No. 9 — paper by P. F. Lett, A. C. Kohler, and D. N. Fitzgerald: *Role of stock biomass and temperature in recruitment of southern Gulf of St. Lawrence Atlantic cod, Gadus morhua.*

Page 1619: Left column, equation IV, delete multiplication sign introducing second line of equation.

VOLUME 32, No. 12 — paper by W. D. Youngs and D. S. Robson: *Estimating survival rate from tag returns: model tests and sample size determination.*

Page 2366: Right column, par. 1, line 4, "E_i*" should be "$\hat{E}_i$*"; line 5, "S_i" should be "$\hat{S}_i$"; line 13 should read "$\hat{\sigma}^2_{\hat{E}_i^*} \doteq \frac{\hat{E}_i^*}{R_i N_i}$."

Page 2367: Left column, par. 3, line 9, "$\sigma_{\hat{S}_1}\sqrt{N}$" should be "$\sigma_{\hat{S}_i}\sqrt{N}$."

Page 2368: Right column, par. 2, "$\sigma_{\hat{S}_i}$" should be "$\sigma_{\hat{S}_i}$" throughout the paragraph; line 2, "1" should be "S"; par. 3, line 1, "$\sigma_{\hat{S}_i}$" should be "$\sigma_{\hat{S}_i}$"; line 5, "$\sigma_{\hat{S}_1}\sqrt{N}$" should be "$\sigma_{\hat{S}_i}\sqrt{N}$"; par. 4, line 8, "$S_i$" should be "$\hat{S}_i$"; Figure 4 caption, line 1 should read "Response of $\sigma_{\hat{S}_i}\sqrt{N}$ as a function."

VOLUME 32, No. 12 — note by M. Busdosh and R. M. Atlas: *Response of two arctic amphipods, Gammarus zaddachi and Boeckosimus (Onisimus) affinis, to variations in temperature and salinity.*

Page 2564–2567: The identity of *Gammarus zaddachi* has been questioned by some amphipod taxonomists. Although the issue is unresolved, the weight of current taxonomic opinion indicates that the species referred to as *G. zaddachi* throughout this Note is probably *Gammarus setosus* Dementieva.

VOLUME 33, No. 1 — paper by F. P. Healey and L. L. Hendzel: *Physiological changes during the course of blooms of Aphanizomenon flos-aquae.*

Page 37: Table 1, line 1 should be Lake 154 instead of Lake 143.

Page 37: Left column, par. 2, line 10 should read "was measured by adding 10 μM K_2HPO_4."

Page 39: Figure 2 caption should read "Changes in some physiological characteristics of *A. flos-aquae* during the course of blooms in lakes 885 and 587 during the summer of 1974. Chlorophyll *a*, soluble reactive P (SRP) and ammonium-N concentrations, kindly provided by Dr J. Barica, are averages of surface and 1.0-m determinations and are given in micrograms per liter. Cellular composition is given in micrograms per milligram dry weight. The protein to carbohydrate ratio is by weight. N and P debts are in micromoles per milligram dry weight. The vertical arrow indicates the onset of collapse".

VOLUME 33, No. 1 — paper by R. J. G. Lester and B. A. Daniels: *The eosinophilic cell of the white sucker, Catostomus commersoni.*

Page 140: Left column, par. 2, line 5 should read "osmic combination (Desser and Lester 1975)."

Page 142: Right column, par. 1, line 3 should read "(Lester and Desser 1975)"; Figure 6 caption should read "(epon section, methylene blue, and safranin)."

Page 143: Left column, par. 2, line 14 should read "(Lester and Desser 1975)."

VOLUME 33, No. 2 — note by G. K. Iwama, G. L. Greer, and P. A. Larkin: *Changes in some hematological characteristics of coho salmon (Oncorhynchus kisutch) in response to acute exposure to dehydroabietic acid (DHAA) at different exercise levels.*

Page 286: Right column, par. 4, line 1 should read "Means and standard errors were calculated for."

Page 287: Table 1, headnote, line 1 should read "Mean clotting time ($\bar{x} \pm S_{\bar{x}}$) in seconds."

Page 288: Table 2, headnote, line 1 should read "Mean total white blood cell count ($\bar{x} \pm S_{\bar{x}}$; no./mm^3 = × 10^4) for controls."

Page 288: Left column, par. 1, line 3 should read "only hemacytometric."

VOLUME 33, No. 4, PART 1 — paper by W. Templeman, V. M. Hodder, and A. M. Fleming: *Infection of lumpfish (Cyclopterus lumpus) with larvae and of Atlantic cod (Gadus morhua) with adults of the copepod, Lernaeocera branchialis, in and adjacent to the Newfoundland area, and inferences therefrom on inshore–offshore migrations of cod.*

Page 726: Figure 5 caption should read "*Lernaeocera branchialis*: distribution of infection of 51–90-cm cod by the adult parasite (percentages of cod infected by one or more parasites)."

Page 728: Figure 7 caption should read "*Lernaeocera branchialis*: distribution of infection of 31–50-cm cod by the adult parasite (percentages of cod infected by one or more parasites)."

VOLUME 33, No. 4, PART 2 — paper by A. H. Weatherley: *Factors affecting maximization of fish growth.*

Page 1050: Left column, par. 4, line 9, the equation should read "$\frac{dw}{dt} = Hw^m - Dw^n$"; Right column, par. 5, line 14, the equation should read "$G = \tau\left[\frac{\gamma v \rho}{1 + \gamma v \rho h}\right] - [z + \alpha v^\beta]$"; line 15 should read "where τ = the portion of the ration ultimately"; insert "ρ = food concentration (cal m^{-3})" between lines 17 and 18.

Page 1051: Left column, par. 1, line 11, delete "(*r*)".

Page 1053: Right column, par. 5, line 4, the equation should read "$\frac{dG}{dN}$ or $\frac{d(\Delta w)}{dN} \propto \frac{I}{N}$". Corrections have been made in the reprint of this paper. These errors occurred during processing of the manuscript and must not be ascribed to the author.

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Influence of food competition, predation, and cannibalism on walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) populations in Lake of the Woods, Minnesota **W. A. Swenson and L. L. Smith Jr.**

Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*) **J. Janssen**

Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption **D. M. Eggers**

Community and species responses of Chironomidae (Diptera) to contamination of fresh waters by crude oil and petroleum products, with special reference to the Trail River, Northwest Territories, Canada **D. M. Rosenberg and A. P. Wiens**

Cadmium and zinc toxicity to flagfish, *Jordanella floridae* **R. L. Spehar**

Contribution of gut contents to the concentration and body burden of elements in *Tipula* spp. from a spring-fed spring **J. W. Elwood, S. G. Hildebrand, and J. J. Beauchamp**

Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens* **M. D. Clady**

Direct and indirect effects of oil on ringed seals (*Phoca hispida*) of the Beaufort Sea **J. R. Geraci and T. G. Smith**

Significance of the timing of initial feeding in hatchery rainbow trout, *Salmo gairdneri* **T. K. Twongo and H. R. MacCrimmon**

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Ecology of euphausiids in the Gulf of St. Lawrence **F. Berkes**

Pollution Symposium — 13th Pacific Science Congress
Sublethal Effects of Pollution on Aquatic Organisms

Preface/Préface **M. Waldichuk**

Current status of sublethal tests of pollutants on aquatic organisms **J. B. Sprague**

Fish tumors and sublethal effects of pollutants **H. F. Stich, A. B. Acton, and C. R. Forrester**

Reentry of 5-year-old stranded Bunker C fuel oil from a low-energy beach into the water, sediments, and biota of Chedabucto Bay, Nova Scotia **J. H. Vandermeulen and D. C. Gordon Jr.**

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Effects of copper on downstream migration, gill atpase, and adaptation to sea water of juvenile coho salmon (*Oncorhynchus kisutch*) **H. W. Lorz and B. P. McPherson**

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Metabolism of single and combined doses of ^{14}C-aldrin and ^{3}H-*p,p'*-DDT by Atlantic salmon (*Salmo salar*) fry **R. F. Addison, M. E. Zinck, and J. R. Leahy**

Improved reagent dispenser for the determination of dissolved oxygen in sea water **C. C. Cunningham, D. D. W. Conrad, J. D. Moffatt, and E. M. Levy**

Diel movement of walleye, *Stizostedion vitreum vitreum*, in West Blue Lake, Manitoba, as determined by ultrasonic tracking **J. R. M. Kelso**

Seasonal growth rates of mooneye (*Hiodon tergisus*) from the Assiniboine River **C. L. Glenn**

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Science for Canada's Atlantic inshore fisheries **F. D. McCracken and R. D. S. Macdonald**

Letters/Lettres

Comment on review of *Marine Geotechnology*, **B. Russak**; Response of the reviewer of *Marine Geotechnology*, **J. D. Milliman**

Book Reviews/Comptes rendus

Sublethal effects of toxic chemicals on aquatic animals (J. H. Koeman and J. J. T. W. A. Strik [ed.]), **J. C. Davis**; Lake Kariba: a man-made tropical ecosystem in central Africa (E. K. Balon and A. G. Coche [ed.]), **R. H. Lowe-McConnell**

RECENT PUBLICATIONS / RÉCENTES PUBLICATIONS

The number following each title in each series refers to the establishments listed at the end of the section.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section.

Recent Studies

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles on investigations published in other periodicals, which henceforth may be obtained in reprint form only from the author or originating establishment.

2187. BOTTA, J. R., AND D. H. SHAW. 1975. Chemical and sensory analysis of roughhead grenadier (*Macrourus berglax*) stored in ice. J. Food Sci. 40: 1249–1252. (9)

2188. HENDZEL, M. R., AND D. M. JAMIESON. 1976. Determination of mercury in fish. Anal. Chem. 48: 926–928. (4)

2189. HASSAN, E. M. 1975. Some effects of river regulation on marginal seas. Ocean Manage. 2: 333–334. (7)

2190. BIGG, M. A., AND H. D. FISHER. 1975. Effect of photoperiod on annual reproduction in female harbour seals, p. 141–144. *In* K. Ronald and A. W. Mansfield [ed.] Biology of the seal; Proc. Symp. held in Guelph, Ont., August 14–17, 1972. Rapp. R. V. Reun. Cons. Int. Explor. Mer 169. (5)

2191. FREEMAN, H. C., G. SANGALANG, J. F. UTHE, AND K. RONALD. 1975. Steroidogenesis *in Vitro* in the harp seal (*Pagophilus groenlandicus*) without and with methyl mercury treatment *in vivo*. Environ. Physiol. Biochem. 5: 428–439. (8)

2192. SMITH, T. G. 1975. Parameters and dynamics of ringed seal populations in the Canadian eastern arctic, p. 281–295. *In* K. Ronald and A. W. Mansfield [ed.] Biology of the seal; Proc. Symp. held in Guelph Ont., August 14–17, 1972. Rapp. P. V. Reun. Cons. Int. Explor. Mer 169. (5)

2193. SHIEH, H. S., AND J. R. MACLEAN. 1976. Blood changes in brook trout induced by infection with *Aeromonas salmonicida*. J. Wildl. Dis. 12: 77–82. (8)

2194. SERGEANT, D. E. 1975. Estimating numbers of harp seals, p. 274–280. *In* K. Ronald and A. W. Mansfield [ed.] Biology of the seal; Proc. Symp. held in Guelph Ont., August 14–17, 1972. Rapp. P. V. Reun. Cons. Int. Explor. Mer 169. (5)

2195. PERCY, R. 1976. Structure of the nongranulated cells in the hypophyseal rostral *Pars distalis* of cyclostomes and actinopterygians. Cell Tissue Res. 166: 185–200. (4)

2196. HARA, T. J. 1976. Effects of pH on the olfactory responses to amino acids in rainbow trout, *Salmo gairdneri*. Comp. Biochem. Physiol. 54A: 37–39. (4)

Récentes études

Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n° 1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes d'études sur des recherches mentionnées dans d'autres périodiques. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

2197. 1976. Structure–activity relationships of amino acids in fish olfaction. Comp. Biochem. Physiol. 54A: 31–36. (4)

2198. HARA, T. J., AND S. MACDONALD. 1976. Olfactory responses to skin mucous substances in rainbow trout *Salmo gairdneri*. Comp. Biochem. Physiol. 54A: 41–44. (4)

2199. ELSON, P. F. 1975. Atlantic salmon rivers, smolt production and optimal spawning: an overview of natural production. Int. Atl. Salmon Found. Spec. Publ. Ser. 6: 96–119. (6)

2200. PARSONS, L. S. 1976. Distribution and relative abundance of roundnose, roughhead and common grenadiers in the Northwest Atlantic. Int. Comm. Northwest Atl. Fish., Sel. Pap. 1: 73–88. (9)

2201. BRUNSKILL, G. J., P. CAMPBELL, S. ELLIOTT, B. W. GRAHAM, AND G. W. MORDEN. 1975. Rates of transport of total phosphorus and total nitrogen in Mackenzie and Yukon River watersheds, N.W.T. and Y.T., Canada. Verh. Int. Ver. Limnol. 19: 3199–3203. (4)

2202. CHANG, P., AND N. B. SNOW. 1975. Aspects of zoobenthos ecology of the Mackenzie Delta, N.W.T. Verh. Int. Ver. Limnol. 19: 1562–1567. (4)

2203. DAVIES, I. J. 1975. Selective feeding in some arctic Chironomidae. Verh. Int. Ver. Limnol. 19: 3149–3154. (4)

2204. HAMILTON, R. D., R. J. FLETT, AND N. E. R. CAMPBELL. 1975. Nitrogen fixation in aquatic environments — a critical study of the acetylene reduction assay. Verh. Int. Ver. Limnol. 19: 2664–2668. (4)

2205. ROSENBERG, D. M., AND A. P. WIENS. 1975. Experimental sediment addition studies on the Harris River, N.W.T., Canada: the effect on macroinvertebrate drift. Verh. Int. Ver. Limnol. 19: 1568–1574. (4)

2206. KESHAVANATH, P., S. K. NAYYAR, B. I. SUNDARARAJ, AND E. M. DONALDSON. 1976. Maintenance of spermatogenesis and seminal vesicles in the hypophysectomized catfish, *Heteropneustes fossilis* (Bloch): effects of ovine and salmon gonadotropin, and testosterone. Can. J. Zool. 54: 285–292. (3)

2207. RUDD, J. W. M., AND R. D. HAMILTON. 1975. Methane oxidation in a eutrophic Canadian Shield Lake. Verh. Int. Ver. Limnol. 19: 2669–2673. (4)

2208. SAETHER, O. A. 1975. Nearctic chironomids as indicators of lake typology. Verh. Int. Ver. Limnol. 19: 3127–3133. (4)

2209. SCHINDLER, D. W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen and carbon. Verh. Int. Ver. Limnol. 19: 3221–3231. (4)

2210. WARWICK, W. F. 1975. The impact of man on the Bay of Quinte, Lake Ontario, as shown by the subfossil chironomid succession (Chironomidae, Diptera). Verh. Int. Ver. Limnol. 19: 3134–3141. (4)

2211. PARSONS, L. S., AND D. G. PARSONS. 1976. Effects of diurnal variation in availability upon estimation of redfish numbers and biomass from stratified-random bottom trawl surveys. Int. Comm. Northwest Atl. Fish., Sel. Pap. 1: 19–29. (9)

2212. MITCHELL, E. D. 1975. Parallelism and convergence in the evolution of Otariidae and Phocidae, p. 12–26. *In* K. Ronald and A. W. Mansfield [ed.] Biology of the seal; Proc. Symp. held in Guelph, Ont., August 14–17, 1972. Rapp. P. V. Reun. Cons. Int. Explor. Mer 169. (5)

2213. BARNES, L. G., AND E. D. MITCHELL. 1975. Late Cenozoic Northeast Pacific Phocidae, p. 34–42. *In* K. Ronald and A. W. Mansfield [ed.] Biology of the seal; Proc. Symp. held in Guelph Ont., August 14–17, 1972. Rapp. P. V. Reun. Cons. Int. Explor. Mer 169. (5)

2214. ELSON, P. F., AND A. L. W. TUOMI. 1975. New basis for rational management. Foyle Fish. p. 1–224. (6)

2215. LOCKHART, W. L., R. WAGEMANN, J. W. CLAYTON, B. GRAHAM, AND D. MURRAY. 1975. Chronic toxicity of a synthetic tri-aryl phosphate oil to fish. Environ. Physiol. Biochem. 5: 361–369. (4)

2216. SUTCLIFFE, W. H. JR., E. A. ORR, AND O. HOLM-HANSEN. 1976. Difficulties with ATP measurements in inshore waters. Limnol. Oceanogr. 21: 145–149. (7)

2217. MASON, J. C., AND S. MACHIDORI. 1976. Populations of sympatric sculpins (*Cottus aleuticus* and *C. asper*) in four adjacent salmon producing coastal streams on Vancouver Island, B.C. Fish. Bull. 74: 131–141. (1)

2218. MASON, J. C. 1976. Some features of coho salmon fry (*Oncorhynchus kisutch*) emerging from simulated redds and concurrent changes in photobehavior. J. Fish Biol. 74: 167–175. (1)

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KRAMER, D. E., AND D. M. A. NORDIN. 1975. Physical data from a study of size, weight, and gonad quality for the Red Sea urchin (*Strongylocentrotus franciscanus* (Agassiz)) over a one-year period. Fish. Mar. Serv. MS Rep. 1372: 91 p. (2)

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1976. Pacific hake and walleye pollock study, Strait of Georgia cruise, A. P. Knight, July 29–31, 1974. Fish. Mar. Serv. MS Rep. 1374: 28 p. (1)

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HUNTER, J. G. 1976. Arctic char and hydroelectric power in the Sylvia Grinnell River. Fish. Mar. Serv. MS Rep. 1376: 21 p. (5)

BEAMISH, R. J., F. P. JORDAN, J. R. SCARSBROOK, AND R. PAGE. 197 . An initial study of fishes inhabiting the surface waters of the Strait of Georgia. M. V. *Caligus*, July–August, 1974. Fish. Mar. Serv. MS Rep. 1377. (1)

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Traductions

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Journal of the Fisheries Research Board of Canada

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Content

We invite submission of manuscripts in the broad field of fisheries management, ocean science, and aquatic environments relevant to Canada.

Articles: Reports of research studies of broad scope that are original contributions to science.

Notes: Differ from papers on the basis of scope or completeness, rather than quality of research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on methodology or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as articles except that they have no centered headings and should occupy no more than four printed pages.

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Letters: Opinion on topics recently under discussion in the *Journal*; preferred maximum length, 500 words. The Editor reserves the right to shorten letters and to make other changes to accord with the style of the *Journal*.

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The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW, Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970), Special Publication No. 6 of the American Fisheries Society.

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Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

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Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

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Journal de l'office des recherches sur les pêcheries du Canada

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Nous désirons reçevoir des manuscrits s'insérant dans le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada.

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Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de reproductions photographiques ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauteur lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de les facturer. Les frais sont de $40.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

Listes de contrôles pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send a photographic reproduction (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal de l'office des recherches sur les pêcheries du Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, le nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit un reproduction photographique (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

Fishes of the World

JOSEPH S. NELSON

An ichthyology book *Fishes of the World* by Joseph S. Nelson of the Department of Zoology, The University of Alberta in Edmonton is being published by John Wiley and Sons (Wiley-Interscience) and should be available by August 1976. The book presents a modern systematic treatment of all major fish groups and is designed for the ichthyology student and others who desire a modern review of, or reference to, fish classification. Alternate schemes of classification are referred to. Descriptive material, including range, is given for all extant fish families (frequently to lower levels). Major extinct groups are also discussed. The number of recognized genera (with examples or full listing) and species are given for the vast majority of families. Some 45 distribution maps, a checklist, and bibliography are also included. The book contains about 420 outline drawings and should be almost 400 pages.

Persons wishing to order the book or wishing to be notified when the book is available should contact:

Dr M. M. Conway
Life Sciences Editor
John Wiley and Sons, Inc.
605 Third Avenue
New York, N.Y. 10016, USA

Fishes of the World

JOSEPH S. NELSON

Un ouvrage d'ichtyologie intitulé *Fishes of the World* par Joseph S. Nelson du département de zoologie de l'université de l'Alberta à Edmonton doit paraître chez John Wiley and Sons (Wiley-Interscience) d'ici août 1976. Conçu à l'intention de l'étudiant en ichtyologie et de tous ceux qui désirent obtenir un aperçu moderne de la classification des poissons, ce livre présente un traitement systématique et moderne de tous les groupes importants. L'auteur se reporte également à d'autres classifications. On trouve, en outre, de l'information descriptive, y compris de l'habitat, sur toutes les familles existantes de poissons (souvent allant jusqu'aux niveaux inférieurs). Il est également question des principaux groupes disparus. Le nombre de genres (avec exemples ou listes complètes) et d'espèces reconnus est fourni pour la grande majorité des familles. L'ouvrage comprend quelque 45 cartes de distribution, une liste de contrôle, une bibliographie et près de 420 croquis. Le livre devrait compter environ 400 pages.

Ceux qui désirent commander cet ouvrage ou être avisés au moment où il devriendra disponible devraient communiquer avec:

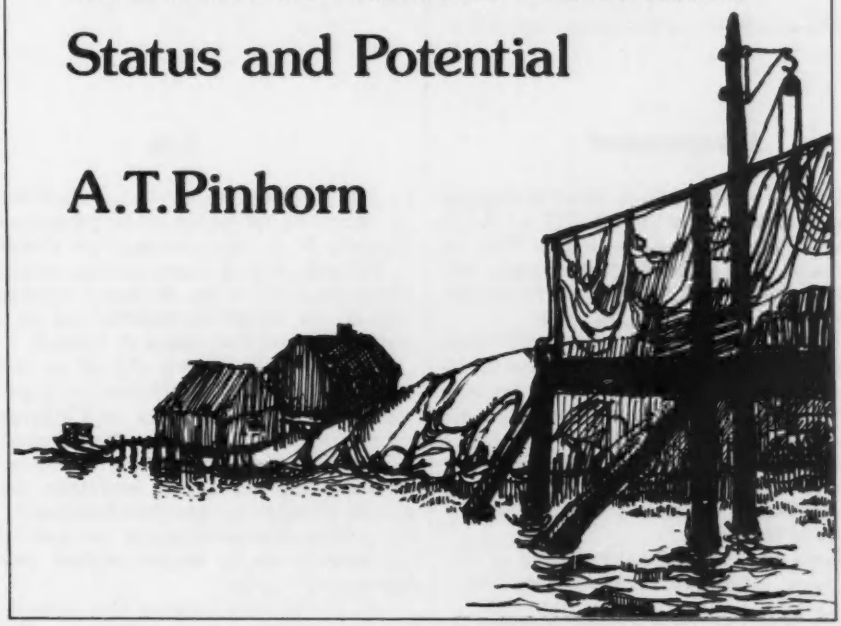
Dr M. M. Conway
Life Sciences Editor
John Wiley and Sons, Inc.
605 Third Avenue
New York, (N.Y.), 10016, USA

Bulletin of the Fisheries Research Board of Canada

Bulletin 194 Ottawa 1976

Living Marine Resources of Newfoundland~Labrador: Status and Potential

A.T.Pinhorn



Knowledge on the marine fisheries resources of Newfoundland and Labrador to 1964 was summarized in Bulletin 154 of the Fisheries Research Board of Canada. Additional information, which has become available since that time, is summarized here. Scientific basis for regulating and managing the international fisheries in the Newfoundland and Labrador area through the International Commission for the Northwest Atlantic Fisheries (ICNAF) is also discussed.

Current information is presented for all species that presently support or have potential for supporting commercial fisheries in the area. Detail given varies depending on the present extent of knowledge and previous coverage of the species. It is presented on a species-by-species basis and, when possible, on a stock-by-stock basis within species. Pertinent information is given on the distribution, abundance, general biology, and fishery of each species, especially where this was not previously covered. Also, since in the late 1960s and 1970s regulations of one form or another have been introduced for many species, an extensive treatment of the management regime for such species is presented. Potential for increased catches from all these resources is summarized.

(Canada: $4.00, Other countries: $4.80; Cat. No. Fs 94-194; 64 pages)

La version française est en préparation

To obtain the publication listed above, at the price indicated, write to:

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Announcement

When *Fishes of the Atlantic Coast of Canada*, Fisheries Research Board Bulletin 155, by A. H. Leim and W. B. Scott, was published in 1966, an early revision was planned. That revision was postponed, however, in favor of *Freshwater Fishes of Canada* (FRB Bulletin 184).

The revision of Bulletin 155 is now under way. The cooperation and support of everyone interested in Atlantic marine fishes is earnestly solicited. Records of unusual occurrences, behavior, or observations on other aspects of the biology, game or commercial importance of the fishes in the region would be welcomed. Comments or criticisms of the original volume itself would also be useful.

Comments may be addressed directly to Dr. W. B. Scott, Huntsman Marine Laboratory, Brandy Cove, St. Andrews, New Brunswick, or to the Department of the Environment, Fisheries and Marine Service, Office of the Editor, Journal of the Fisheries Research Board of Canada, 116 Lisgar St., Ottawa K1A 0H3.

Avis

Lors de la publication, en 1966, du bulletin nº 155 de l'Office des recherches sur les pêcheries intitulé *Poissons de la côte atlantique du Canada*, par A. H. Leim et W. B. Scott, on avait projeté de le réviser sous peu. Cette révision a cependant été retardée en faveur du bulletin 184 de l'ORP, intitulé *Poissons d'eau douce du Canada*.

La révision du bulletin 155 est en cours. La collaboration et l'appui de tous ceux qui s'intéressent aux espèces marines de l'Atlantique seraient grandement appréciés. Tout compte rendu de faits inhabituels, de comportements ou d'observations d'autres aspects importants des poissons de la région sur les plans biologique, sportif ou commercial serait bienvenu. Les commentaires ou critiques sur le volume original pourraient également être utiles.

Les commentaires peuvent être adressés directement à M. W. B. Scott, Laboratoire Huntsman de sciences marines, anse Brandy, St. Andrews (Nouveau-Brunswick) ou au Ministère de l'Environnement, Service des pêches et des sciences de la mer, Bureau du rédacteur du Journal de l'Office des recherches sur les pêcheries, 116, rue Lisgar, Ottawa K1A 0H3.

Book Reviews/Comptes rendus

Heavy metals in the aquatic environment. An international conference (P. A. Krenkel [ed.]). **P. V. Hodson**; Statistical calculations — how to solve statistical problems (E. J. Middlebrooks). **J. A. Thomson** 1865–1866

Corrections to recent publications/Corrections sur récentes publications 1867–1868
Coming next month/À paraître le mois prochain 1869–1870
Recent publications/Récentes publications 1871–1876
Guide for authors and typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–v*

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Chlorinated guaiacols in bleachery wastes: comments on a paper by Leach and Thakore, **I. H. Rogers;** Response to the comments of I. H. Rogers, **J. M. Leach and A. N. Thakore;** Discussion of benthic aspects of "Perspectives" November 1975, **D. V. Ellis;** Reply to D. V. Ellis's comments on a prognosis for Canadian benthic biological oceanography, **C. D. Levings** 1858–1864

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